

# An Evolutionary Theory for the Variability Hypothesis

Theodore P. Hill

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## Abstract

An elementary mathematical 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 tend to prevail over those with lesser variability; and conversely, 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 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 statistical model using normally distributed 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 reported “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” [11, 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.[8]). Almost exactly one hundred years after Darwin’s observation, specifically citing Darwin’s research on animals [11, pp. 221–27] and Ellis’s research on humans [15, pp. 358–372], one expert concluded “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*” [46, pp. 772-73, emphasis added].

The past quarter century has produced much new research on the greater male variability hypothesis in different contexts, most of which refer to humans. These include primary studies with findings that are consistent with the hypothesis (e.g., [2], [3], [4], [5], [6], [7], [9], [12], [13] [17], [18], [22], [23], [25], [26], [30], [34], [36], [37], [39], [40], [41], [43], [44], [48], [51]); primary studies with findings inconsistent with the hypothesis (e.g., [16], [31], [35], [42]); primary studies with findings that are mixed (e.g., [17], [18], [24], [25]); and meta-analyses of studies on the variability hypothesis (e.g., [22], [27], [29], [32], [33], [38], [47]). For direct quotes from each of these references, see Appendix A.

## 2 A theory for gender differences in variability

After citing specific evidence of greater male variability, Darwin had 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”

[11, p. 224]. This question has persisted into the 21st century; for instance, “There is evidence of slightly greater male variability in scores, although the causes remain unexplained” [30, p. 495], and “the reasons why males are often more variable remain elusive” [22, 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” [50, p. 255].

The objective of this paper is to provide an elementary mathematical theory based on several biological principles that might help explain how a difference in variability could naturally evolve between two sexes of the same species. 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 (less 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 theory makes no assumptions about differences in means between the sexes, nor does it presume that one sex is selective and the other non-selective. In contrast to other related notions such as “the sex that experiences more intense...vetting by the other sex will tend to show greater within-sex variation on many traits” [20, p. 176], the selectivity theory above does not rely on comparisons between the sexes. If both sexes of a species happen to be selective, for instance, then the selectivity theory predicts that the best evolutionary strategy for each is to tend toward greater variability.

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. As will be seen below, for example, if by “variability” is meant “statistical variance” or “standard deviation”, then this principle is not true in general, although it does hold for normal (Gaussian, or bell-shaped) distributions. First, the following informal hypothetical example may help convey the intuition behind this principle.

**Example 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  $B_1$  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 1(a)). 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 1(b)). 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 1(c)).

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 1(d)). 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

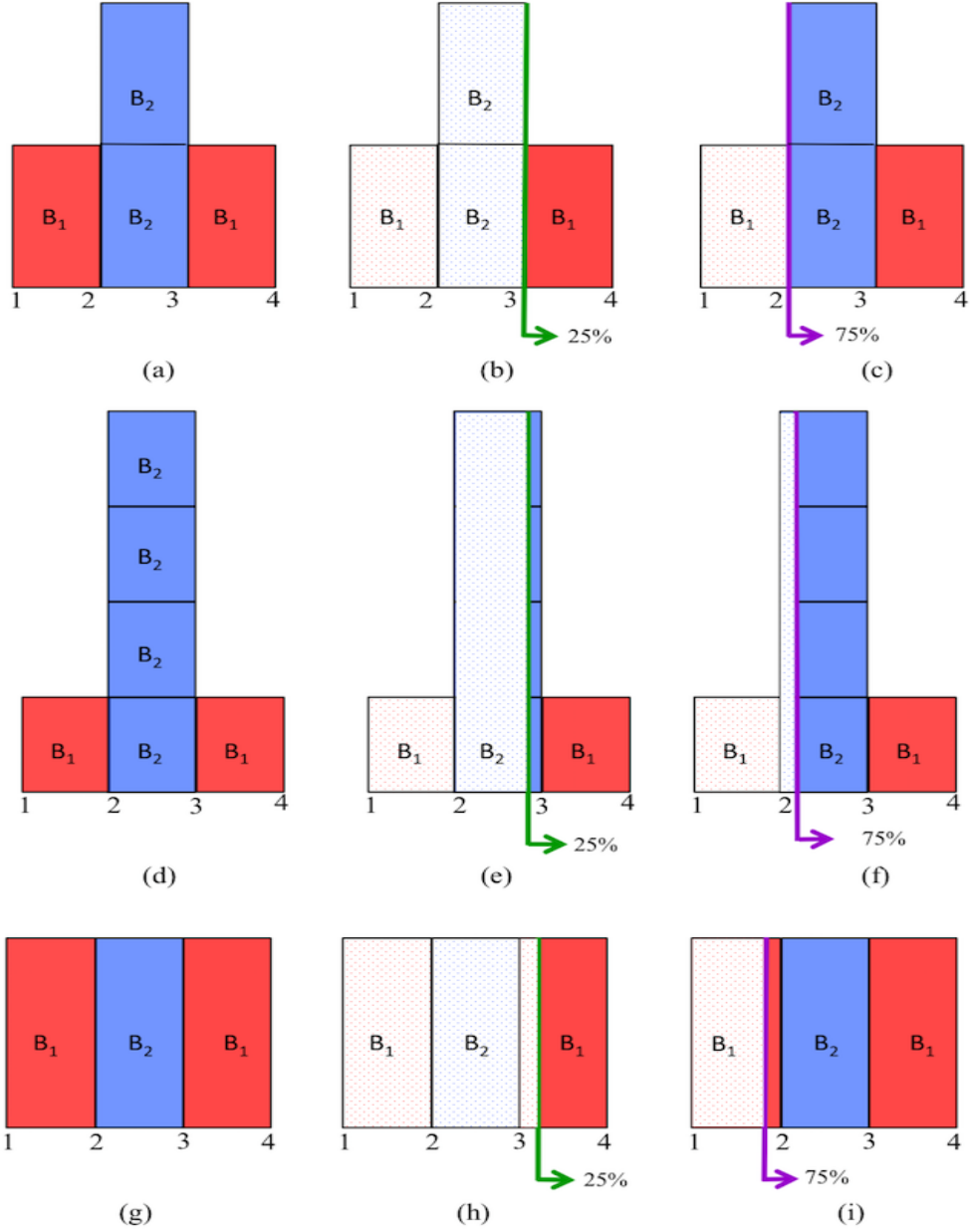


Figure 1: The three cases of Example 1: The red blocks represent the distribution of the more variable subpopulation  $B_1$  of sex  $B$ , and the blue represent the less variable subpopulation  $B_2$ .

on the initial distribution, the more variable subpopulation will be overrepresented (Figure 1(e)). 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 1(f)).

*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 1(g)). 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 1(h)), 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 1(i)).

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 and variability

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 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 ([10], [45]).

The actual magnitudes of these desirability values are assumed to have no significance, 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  $B$ .

Next, to address the notion of gender differences in variability between two subpopulations in their desirability to the opposite sex, the notion of one distribution being more (or less) variable than another must be specified. There are many possibilities for such a definition, for instance via comparisons of statistical variance or standard deviations or first absolute central moments, but those can be very misleading in this setting since a single outlier can dramatically alter the value of such statistics. On the other hand, basic comparisons of the tails of two different 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*  $P_2$  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,  $P_1$  is more variable than  $P_2$  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, also called the survival function, of  $P$ . That is,  $S_P : \mathbb{R} \rightarrow [0, 1]$  is defined by  $S_P(x) = P(x, \infty)$  for all  $x \in \mathbb{R}$ , so  $S_P(x)$  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. Similarly, in this simple model it is assumed that the populations are large and mobile so there are always available potential mates of the opposite sex above the threshold desirability cutoff.

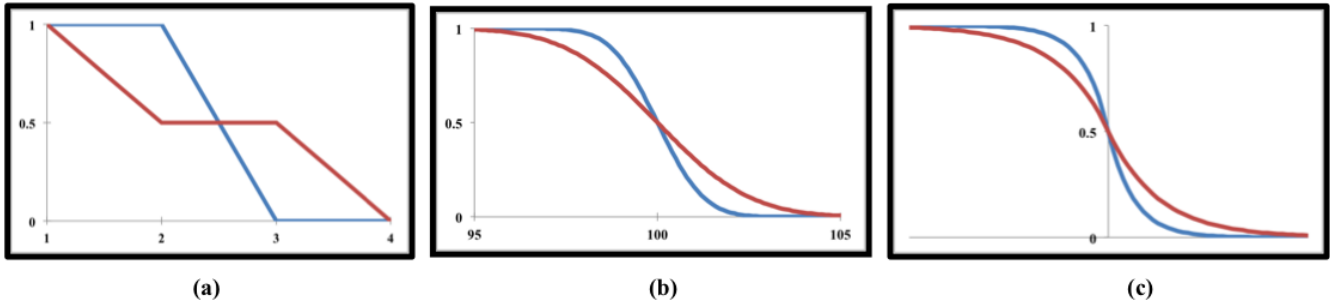


Figure 2: The survival functions and comparative variability of three pairs of distributions: the uniform distributions in Example 1 above; the normal distributions in Example 2 below; and the Laplace (double-exponential) distributions in Example 3. In each case, the red curves denote the more variable 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 clearly prevail if the opposite sex is selective.

As a very important special case, the comparison of variability in this sense between two normal (Gaussian, or bell-shaped) distributions with the same average value is *equivalent* to comparisons of standard deviation. Letting  $N(\mu, \sigma^2)$  denote a normal distribution with mean  $\mu$  and standard deviation  $\sigma$ , it can be shown using elementary properties of the gaussian distribution (see Proposition 7.1 below) that  $N(\mu, \sigma_1^2)$  is more variable than  $N(\mu, \sigma_2^2)$  if and only if  $\sigma_1^2 > \sigma_2^2$ .

Using these definitions of variability and selectivity, two mathematical models for the selectivity-variability principle above will now be presented.

## 4 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 they have identical medians  $m$ . If  $B_1$  is more variable than  $B_2$ , i.e., if  $P_1$  is more variable than  $P_2$ , then it can be shown (see Proposition 7.2 below) that, for

all  $\beta$ , if sex  $A$  is selective, that is, if  $p_A < 0.5$ , then the probability that a random individual from  $B_1$  is selected for mating by sex  $A$  is greater than the probability that a random individual from  $B_2$  is selected; and conversely, if sex  $A$  is non-selective, then the probability that a random individual from  $B_2$  is selected for mating by sex  $A$  is greater than the probability that a random individual from  $B_1$  is selected.

**Example 2.** 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 7.1 below,  $N(\mu, \sigma_1^2)$  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.

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 1.

Thus, in this discrete-time setting, if one sex remains selective from each generation to the next, for example, then in each successive generation more variable subpopulations of the opposite sex will prevail over less variable subpopulations with comparable average desirability. Although the desirability distributions themselves may evolve, if greater variability prevails at each step, that suggests that over time the opposite sex will tend toward greater variability.

## 5 A continuous-time deterministic model

In this model, 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 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

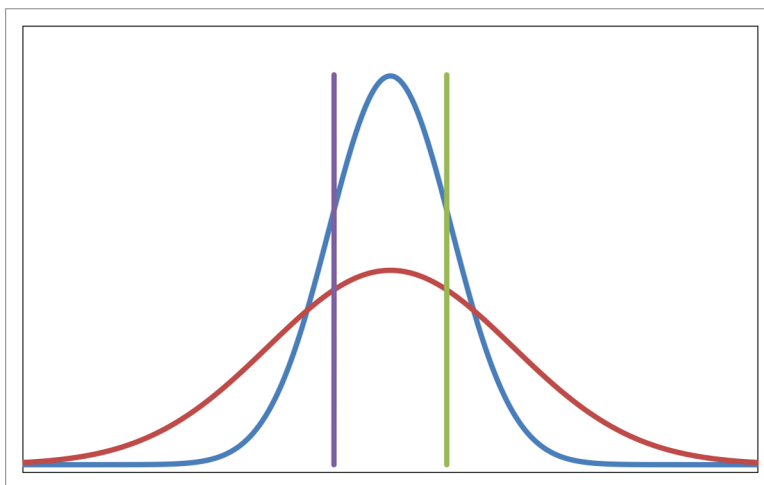


Figure 3: The red curve is the desirability distribution of the more variable normal subpopulation  $B_1$  in Example 2 and the blue curve is the desirability distribution of the less variable subpopulation  $B_2$ . The vertical green line is the threshold cutoff for the opposite sex  $A$  so that exactly 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.

half of each subpopulation  $B_1$  and  $B_2$  has desirability value above the  $m$  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,

$$(1) \quad \frac{d(x_1 + x_2)}{dt} = p_A(x_1 + x_2).$$

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.,

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

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 (2) is closely related to the classical replicator equation (cf. [28], [49]), 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 the selectivity cutoffs.

Suppose that  $P_1$  is more variable than  $P_2$ . Then it can be shown (see Proposition 7.3 below) that 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 that 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.

**Example 3.** Let the survival functions  $S_1$  and  $S_2$  for subpopulations  $B_1$  and  $B_2$  be standard symmetric double-exponential (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). Here subpopulation  $B_1$  is clearly more variable than  $B_2$ .

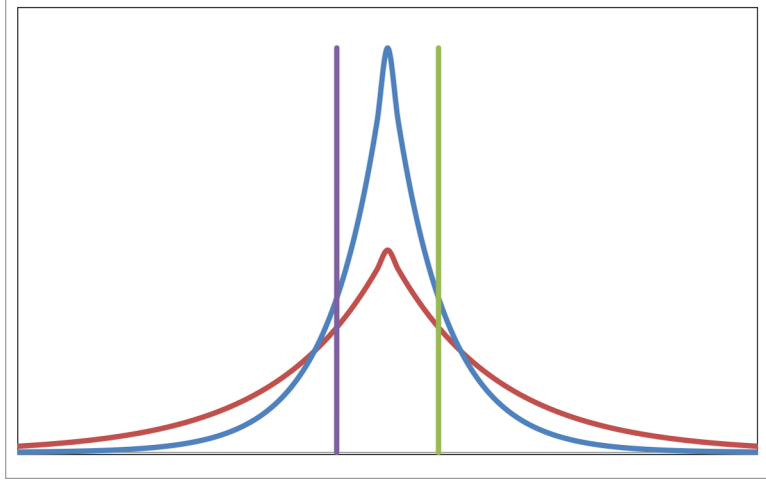


Figure 4: The red curve is the density of the desirability value of the more variable subpopulation  $B_1$  in Example 3, and the blue curve is the density of the less variable subpopulation  $B_2$ . If  $B_1$  and  $B_2$  are of equal size, then the vertical green line is the threshold cutoff for the 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.

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 (1) and (2), and noting that  $S_2(x) = 2S_1^2(x)$  for  $x \geq 0$  yields the following coupled system of ordinary differential equations:

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

Figure 5 illustrates a numerical solution of (3) 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 in the most desirable three-quarters of sex  $B$ , i.e.,  $p_A = 0.75$ . Using (1) and (2) again, and noting that  $S_2(x) = 4S_1(x) - 2S_1^2(x) - 1$



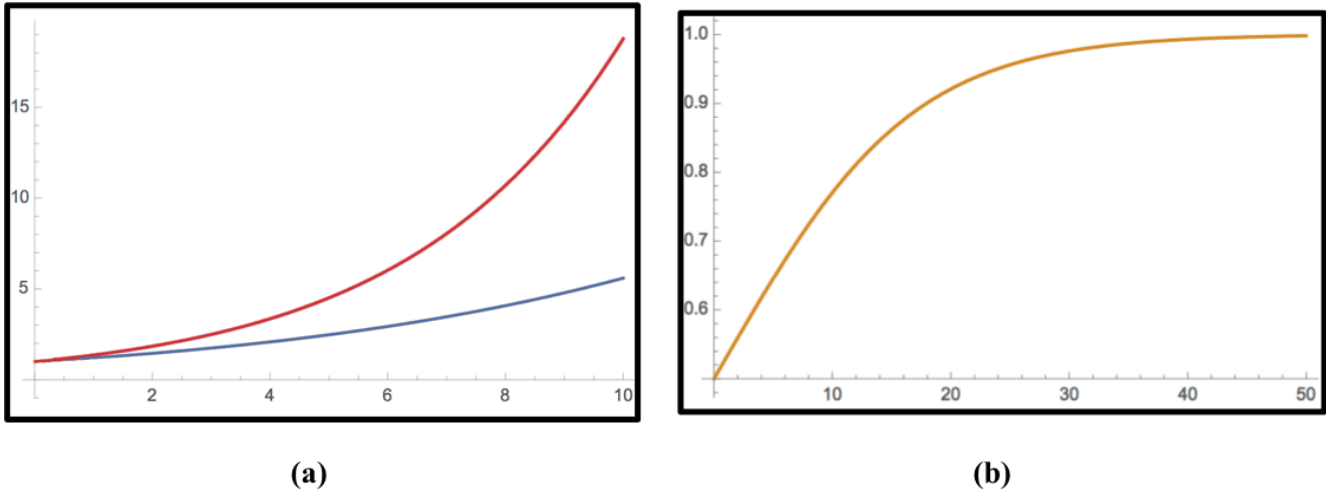


Figure 5: Selective case – Population sizes and ratio. The graphs of the more variable  $x_1(t)$  in red and  $x_2(t)$  in blue (a) and the ratio  $x_1(t)/(x_1(t) + x_2(t))$  (b) satisfying (3).

for  $x \leq 0$  yields the following system:

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

Figure 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  $B_1$ .

Note 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.

## 6 Selectivity, parenting, and greater male variability

The selectivity-variability principle introduced above 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” [19, p. 273]. For example, “When females invest more in

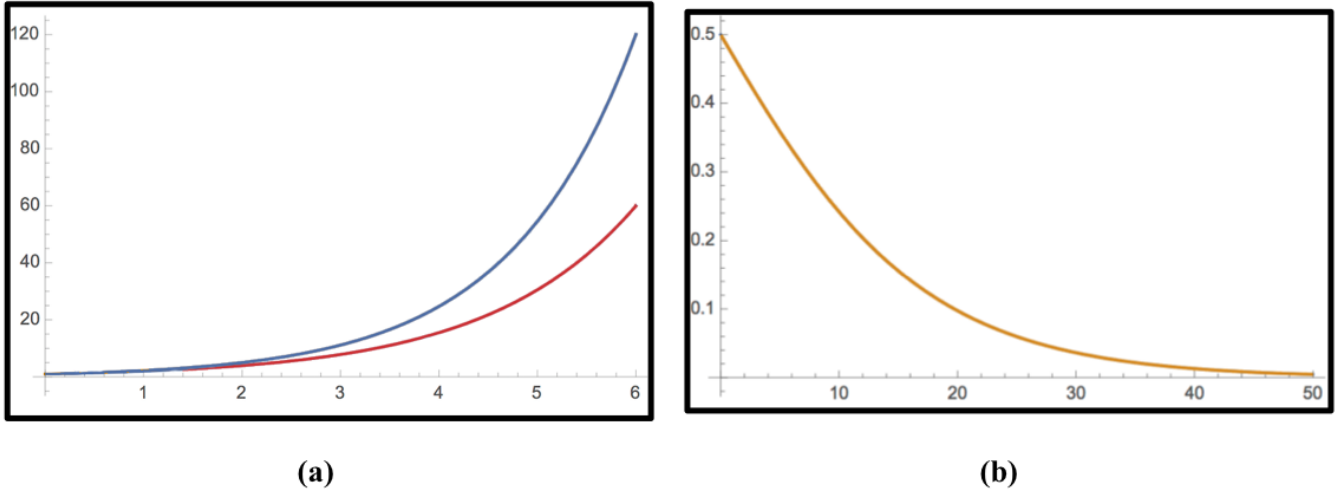


Figure 6: Non-selective case – Population sizes and ratio. The graphs of the more variable subpopulation size  $x_1(t)$  in red and less variable  $x_2(t)$  in blue (a), and the ratio  $x_1(t)/(x_1(t) + x_2(t))$  (b) satisfying (4).

offspring than males, parental investment theory says that selection operates so that females discriminate among males for mates...and males are indiscriminate” [21, p. 2037]; see also [14]. 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 [1, p. 300].

The second additional biological tenet is gender-parenting, which says that “typical species [have] less parental investment by males than females” [21, p. 2037] which occurs, for example, in more than ninety-five percent of mammalian species [20, 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 many species generally invest more in parenting than males, so by the parenting-selectivity tenet females will generally be relatively selective and males relatively non-selective, and 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 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.

The theory of differences in gender variability introduced here could help explain how current greater or lesser variability might depend on the past selectivity factor of the opposite sex, and pertains equally to any sexually dimorphic species and either sex. Moreover, if this selectivity theory has some validity, then gender differences in variability are time dependent whenever the two sexes’ tendencies in selectivity are evolving. If gender differences in selectivity have been decreasing and are now less significant in some species than they were in prehistoric times, then this theory could also predict that the gender difference in variability in those species has also been decreasing. One recent meta-analysis found empirical evidence of exactly that trend in humans, reporting “The gender difference in variability has reduced substantially over time within the United States” [47, p. 8].

## 7 Proofs

### 7.1 Probabilistic model proofs

The following simple proposition may be well known, but since no reference is known to the author, a proof is included for completeness.

**Proposition 7.1.**  $N(\mu, \sigma_1^2)$  is more variable than  $N(\mu, \sigma_2^2)$  if and only if  $\sigma_1^2 > \sigma_2^2$ .

*Proof.* Let  $X_1 \sim N(\mu, \sigma_1^2)$  and  $X_2 \sim N(\mu, \sigma_2^2)$ , and 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.  $\square$

To establish the following discrete-time probabilistic model result, suppose that sex  $B$  of a given hypothetical species consists 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. (Note the key assumption that the average values, i.e. the medians, are the same.)

**Proposition 7.2.** Suppose subpopulation  $B_1$  is more variable than  $B_2$ , i.e.,  $P_1$  is more variable than  $P_2$ , and that the proportion of  $B$  that is the more variable  $B_1$  is  $\beta \in (0, 1)$ . Then

- (i) If  $p_A < 0.5$ , i.e., if sex  $A$  is selective, then the probability that a random individual from  $B_1$  is selected for mating by sex  $A$  is greater than the probability that a random individual from  $B_2$  is selected.
- (ii) If  $p_A > 0.5$ , i.e., if sex  $A$  is non-selective, then the probability that a random individual from  $B_2$  is selected for mating by sex  $A$  is greater than the probability that a random individual from  $B_1$  is selected.

*Proof.* Fix  $\beta \in (0, 1)$ , let  $X_1$  and  $X_2$  denote the desirability values for an individual drawn at random from  $B_1$  and  $B_2$ , respectively, and let  $S_1$  and  $S_2$  denote the desirability survival functions for  $X_1$  and  $X_2$ . First, it will be shown that there exists a unique ‘‘threshold’’ desirability cutoff  $c^* \in \mathbb{R}$  such that

$$(5) \quad \begin{aligned} &\beta S_1(c^*) + (1 - \beta)S_2(c^*) = p_A; \text{ and} \\ &c^* > m \text{ if } p_A < 0.5 \text{ and } c^* < m \text{ if } p_A > 0.5. \end{aligned}$$

To see (5), 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) 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  $p_A > 0.5$ .

Next, note that from (5) and the definitions of  $p_A$ ,  $\beta$  and  $c^*$ , it follows that

$$(6) \quad X_i \text{ is acceptable to sex } A \text{ if and only if } X_i \geq c^*, i = 1, 2.$$

To see (i), assume that  $p_A < 0.5$  and note that

$$P(X_1 \text{ is acceptable to sex } A) = S_1(c^*) > S_2(c^*) = P(X_2 \text{ is acceptable to sex } A),$$

where the first and last equalities follow by (6), and the inequality since  $B_1$  is more variable than  $B_2$ . Conclusion (ii) follows analogously. This completes the proof.  $\square$

## 7.2 Deterministic model proof

Recall that in this setting sex  $B$  consists of two growing subpopulations  $B_1$  and  $B_2$  whose sizes at time  $t$  are  $x_1(t)$  and  $x_2(t)$ , respectively, where both functions are assumed to be strictly increasing and differentiable, and the distributions of desirability of  $B_1$  and  $B_2$  individuals (to sex  $A$ ) are given by probabilities  $P_1$  and  $P_2$  that do not change with time or with the sizes of the subpopulations. Furthermore, the respective survival functions  $S_1$  and  $S_2$  are both assumed to be continuous and strictly decreasing with identical (unique) medians  $m$ .

**Proposition 7.3.** Suppose subpopulation  $B_1$  is more variable than  $B_2$ , i.e.,  $P_1$  is more variable than  $P_2$ .

(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  $B_2$ ,

$$(7) \quad \frac{1}{x_1} \frac{dx_1}{dt} > \frac{1}{x_2} \frac{dx_2}{dt}.$$

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  $B_1$ ,

$$(8) \quad \frac{1}{x_2} \frac{dx_2}{dt} > \frac{1}{x_1} \frac{dx_1}{dt}.$$

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

*Proof of (i).* Analogous to the argument for Proposition 7.2, 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  $t > 0$ , (2) implies (7).

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 (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. □

## 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 precise formal definitions and assumptions made here are clearly not applicable in real-life scenarios, and thus the contribution here is also merely a general theory intended to open the discussion to further mathematical 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 individual's 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” [2, 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” [3, 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” [4, 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” [5, 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” [6, p. 371].

“the variances in the personality descriptions by informants were higher for male than for female targets” [7, p. 142].

“greater variation does occur in the males” [9, p. 31].

“Boys were over-represented at the low and high extremes of cognitive ability” [13, p. 533].

“Males have only a marginal advantage in mean levels...but substantially greater variance” [12, p. 451].

“Males were consistently more variable than females in quantitative reasoning, spatial visualization, spelling, and general knowledge” [17, 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” [18, p. 90].

“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” [22, p. 1].

“the variability analyses tended to support the Greater Male Variability Hypothesis” [23, 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” [25, 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” [26, 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” [30, 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” [34, p. 85, p. 88].

“Overall, the results were consistent with previous research, showing small mean differences in the three domains, but considerably greater variability for males” [36, 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” [37, pp. 198, 204–205].

“With one exception...all variance ratios were greater than 1.0” [39, 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” [40, pp. 1331–1332].

“Seven international tests revealed that on average the variance for males was 12% larger than that for females” [41, 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” [43, p. 651].



“There was generally greater male variance across structural measures [in the human brain]” [44, 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” [48, 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” [51, p. 1].

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

“Boys were not found to be more variable than girls” [16, 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” [31, 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” [35, p. 14].

“the common assumption that males have greater variance in mathematics achievement is not universally true” [42, 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” [17, 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” [18, p. 81].

“whether males or females exhibit more variability depends on the domain under consideration” [24, 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” [25, p. 883].

## A.4 Meta-Analyses

“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” [22, 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” [27, 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 women]...Similarly, for verbal performance, variance ratios range between 1.03 and 1.16” [29, 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” [32, 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” [33, 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]” [38, 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” [47].

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