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# HEAVY-TAILEDNESS AND THRESHOLD SEX DETERMINATION\*

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## ABSTRACT

This paper studies the properties of the sex ratio in two-period models of threshold (e.g., polygenic or temperature-dependent) sex determination under heavy-tailedness in the framework of possibly skewed stable distributions and their convolutions. We show that if the initial distribution of the sex-determining trait in such settings is moderately heavy-tailed and has a finite first moment, then an excess of males (females) in the first period leads to the same pattern in the second period. Thus, the excess of one sex over the other one accumulates over two generations and the sex ratio in the total alive population in the second period cannot stabilize at the balanced sex ratio value of  $1/2$ . These properties are reversed for extremely heavy-tailed initial distributions of sex-determining traits with infinite first moments. In such settings, the sex ratio of the offspring oscillates around the balanced sex ratio value and an excess of males (females) in the first period leads to an excess of females (males) in the second period. In addition, the sex ratio in the total living population in the second period can stabilize at  $1/2$  for some extremely heavy-tailed initial distributions of the sex-determining trait. The results in the paper are shown to also hold for bounded sex-determining phenotypes.

*Keywords and phrases:* Multifactorial inheritance models; Threshold sex determination; Temperature-dependent sex determination; Phenotypic traits; Heritability; Sex ratio; Heavy-tailed distributions

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# 1 Introduction and discussion

## 1.1 Objectives and key results

A number of modern species exhibit, to a larger or smaller extent, threshold systems of sex determination. Under such mechanisms, a sex response trait is determined by a continuous phenotype or environmental variable  $X$  (such as size, fitness, exposure to sunlight, food resources, temperature, humidity, etc.). An individual with  $X = \tilde{x}$  becomes a male if the value of  $\tilde{x}$  is greater than a certain threshold level, and a female otherwise.

For instance, in many reptile species sex determination mechanism is temperature dependent: the sex of an embryo is determined by incubation temperature (see Bull, 1981, Cherfas and Gribbin, 1985, Ch. 5, Bull and Charnov, 1989, and Janzen and Paukstis, 1991). In many turtles embryos hatch as males in cool and as females in warm conditions, with a sharp transition from all-male to all-female broods. Alligators, crocodiles and some lizards exhibit the opposite pattern in sex determination: males develop at warm and females at cool temperatures. The inheritance mechanisms where an offspring sex is determined by environmental conditions after conception are referred to as environmental mechanisms of sex determination (e.g., Bulmer and Bull, 1982, Karlin, 1984, Karlin and Lessard, 1986, and Janzen and Paukstis, 1991).

Some patterns of threshold sex determination are also present in humans and other mammals, with parental hormonal levels, diseases, or other variables being responsible for a part of the variation of sex ratio in the offspring. For instance, many studies have also found evidence that mammalian and, in particular, human, sex ratios at birth are partially controlled by parental hormone levels at the time of conception, high levels of androgens and oestrogens and low levels of gonadotrophin and progesterone being associated with male offspring (see James, 1995, 1997, Grant, 1996, and the reviews in James, 1994, 1996). These studies have suggested that hormone levels are responsible for the association between the sex ratios of the offspring in humans and parental dominance, occupation of parents, psychological stress, several illnesses, and, partly, parental socioeconomic status found in numerous works.<sup>1</sup> At the same time, Edlund (1999) indicates that prenatal sex determination and sex selective abortion and postnatal discrimination appear to have a larger order of magnitude in affecting the observed variations in the sex ratio in humans than the parental hormone levels. Threshold sex determination provides a natural framework for modeling dependence of sex ratio in humans on the traits in the above settings, with the sex-determining trait  $X$  being the parental hormonal level, hepatitis infection indicator variable, wealth or income, etc.

Usually (see Bulmer and Bull, 1982, Karlin, 1984, and Karlin and Lessard, 1986), temperature-dependent and, more generally, threshold sex determination with the sex-determining trait  $X$  is modeled by the time series

$$X_{t+1} = (X_t^p + X_t^m)/2, \tag{1}$$

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<sup>1</sup>See also Oster (2005) who argues that high Hepatitis B rates may be responsible for highly skewed sex ratios in several Asian countries.

$t = 0, 1, \dots$ , where  $X_{t+1}$  is the trait value of the offspring; and  $X_t^p$  and  $X_t^m$ ,  $t = 0, 1, 2, \dots$ , are, respectively, paternal and maternal contributions given by independent random variables (r.v.'s) with the non-identical cdf's

$$P(X_t^p \leq x) = P(X_t \leq x | X_t > K), \quad P(X_t^m \leq x) = P(X_t \leq x | X_t \leq K), \quad (2)$$

$K \in \mathbf{R}$ ,  $t = 0, 1, \dots$ .<sup>2</sup> In time series (1), (2), an individual with the value of the sex-determining trait  $X$  equal to  $\tilde{x}$  becomes a male if  $\tilde{x}$  is greater than the threshold level  $K$ , and a female otherwise.

One of the main problems of interest in models of threshold sex determination (1), (2) is how the sex ratio  $r_t$  given by the tail probability  $r_t = P(X_t > K)$  changes with time. This paper studies the properties of the sex ratio  $r_t$  in two-period models (1), (2) under heavy-tailedness in the framework of (possibly skewed) stable distributions and their convolutions.

We show that if the initial distribution of the sex-determining trait is moderately heavy-tailed and has a finite first moment, then the behavior of the sex ratio  $r_t$  in two-period models (1), (2) is the same as in the case of (extremely light-tailed) log-concave densities analyzed by Karlin (1984, 1992). Namely, under such assumptions, an excess of males (females) in the initial period leads to the same pattern in the second period (Theorem 1). Thus, the excess of one sex over the other one accumulates over two generations and the sex ratio in the total alive population in the second period cannot stabilize at the balanced sex ratio value of  $1/2$ .

We further demonstrate that the above properties are reversed in two-period models (1), (2) for extremely heavy-tailed distributions of sex-determining traits with infinite first moments. In such settings, the sex ratio of the offspring oscillates around the balanced sex ratio value and an excess of males (females) in the initial period leads to an excess of females (males) in the second period (Theorem 2). Theorem 3 provides the results on the distances from the sex ratio values in heavy-tailed two-period models (1), (2) to the balanced value  $r = 1/2$ . This theorem implies, in particular, that, for some extremely heavy-tailed initial distributions of the sex-determining trait, the sex ratio in the total living population in the second period can stabilize at the balanced level  $r = 1/2$  (relation (10)). Theorem 4 provides extensions of the results in the paper to the case of bounded sex-determining traits (see also Remark 2 concerning extensions to dependence).

The arguments in the paper exploit the results on comparisons of tail probabilities of heavy-tailed r.v.'s obtained in Ibragimov (2005, 2007a) and asymptotic expansions for stable cdf's (see Appendix A1). The tail probability comparisons for heavy-tailed r.v.'s were used recently in Ibragimov (2007b) to study the propagation of distributional properties of phenotypes in inheritance models (1) and their multisex analogues where the parental contributions  $X_t^p$  and  $X_t^m$  are assumed to be independent and *identically distributed*. The i.i.d. assumption in Ibragimov (2007b) is in contrast to assumption (2). This is because (2) implies the property that the distributions of  $X_t^p$  and  $X_t^m$  are *different* that complicates the analysis of threshold sex determination models, especially in multiperiod settings (see Section 4). In particular, sharp inequalities for (conditional) tail probabilities of linear combinations

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<sup>2</sup>Time series (1) with the parental contributions given by (2) are also used to model polygenic sex determination with a large number of factors (loci) contributing to sex expression; such mechanism of sex determination is exhibited by, e.g., several fish species (see Bacci, 1965, and Karlin and Lessard, 1986).

of the r.v.'s in models (1), (2) are needed for comparisons of the sex ratios in different periods (see the proof of Theorems 1 and 2). The analysis of the distances of the sex ratios from the balanced value  $r = 1/2$  over different periods requires asymptotic approximations to (conditional) distributions of the variables in (1), (2) and their sums (see the proof of Theorem 3).

The paper is organized as follows: Section 2 contains notation and definitions of classes of distributions used throughout the paper and reviews their basic properties. In Section 3, we present the main results on the properties of two-period threshold sex determination models under heavy-tailedness of sex-determining traits' distributions. Section 4 makes some concluding remarks and discusses suggestions for further research. Appendix A1 presents auxiliary results on comparisons and the asymptotics of tail probabilities of heavy-tailed r.v.'s needed for the analysis in the paper. Appendix A2 contains proofs of the results obtained.

## 2 Notation and classes of distributions

The classes of distributions in this section were introduced in Ibragimov (2005, 2007b).

We say that a r.v.  $X$  with density  $f : \mathbf{R} \rightarrow \mathbf{R}$  and the convex distribution support  $\Omega = \{x \in \mathbf{R} : f(x) > 0\}$  is log-concavely distributed if  $\log f(x)$  is concave in  $x \in \Omega$ , that is, if for all  $x_1, x_2 \in \Omega$ , and any  $\lambda \in [0, 1]$ ,  $f(\lambda x_1 + (1 - \lambda)x_2) \geq (f(x_1))^\lambda (f(x_2))^{1-\lambda}$  (see An, 1998). A distribution is said to be log-concave if its density  $f$  satisfies the above inequality. Examples of log-concave distributions include (see, for instance, Marshall and Olkin, 1979, p. 493) normal, uniform, exponential and logistic distributions, the Gamma distribution  $\Gamma(\alpha, \beta)$  with the shape parameter  $\alpha \geq 1$ , the Beta distribution  $\mathcal{B}(a, b)$  with  $a \geq 1$  and  $b \geq 1$ ; and the Weibull distribution  $\mathcal{W}(\gamma, \alpha)$  with the shape parameter  $\alpha \geq 1$ . If a r.v.  $X$  is log-concavely distributed, then its density has at most an exponential tail, that is,  $f(x) = o(\exp(-\lambda x))$  for some  $\lambda > 0$ , as  $x \rightarrow \infty$  and all the power moments  $E|X|^\gamma$ ,  $\gamma > 0$ , of the r.v. exist (see Corollary 1 in An, 1998). This implies, in particular, that distributions with log-concave densities *cannot* be used to model heavy-tailed phenomena. In what follows,  $\mathcal{LC}$  stands for the class of symmetric log-concave distributions.<sup>3</sup>

For  $0 < \alpha \leq 2$ ,  $\sigma > 0$ ,  $\beta \in [-1, 1]$  and  $\mu \in \mathbf{R}$ , we denote by  $S_\alpha(\sigma, \beta, \mu)$  the stable distribution with the characteristic exponent (index of stability)  $\alpha$ , the scale parameter  $\sigma$ , the symmetry index (skewness parameter)  $\beta$  and the location parameter  $\mu$ . That is,  $S_\alpha(\sigma, \beta, \mu)$  is the distribution of a r.v.  $X$  with the characteristic function

$$E(e^{ixX}) = \begin{cases} \exp\{i\mu x - \sigma^\alpha |x|^\alpha (1 - i\beta \text{sign}(x) \tan(\pi\alpha/2))\}, & \alpha \neq 1, \\ \exp\{i\mu x - \sigma |x| (1 + (2/\pi)i\beta \text{sign}(x) \ln|x|)\}, & \alpha = 1, \end{cases}$$

$x \in \mathbf{R}$ , where  $i^2 = -1$  and  $\text{sign}(x)$  is the sign of  $x$  defined by  $\text{sign}(x) = 1$  if  $x > 0$ ,  $\text{sign}(0) = 0$  and  $\text{sign}(x) = -1$  otherwise. The monographs by Zolotarev (1986), Embrechts *et al.*, 1997, and Beirlant *et al.*, 2004, contain detailed reviews of properties of stable and other heavy-tailed distributions. We write  $X \sim S_\alpha(\sigma, \beta, \mu)$ , if the r.v.  $X$  has the stable distribution  $S_\alpha(\sigma, \beta, \mu)$ .

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<sup>3</sup> $\mathcal{LC}$  stands for "log-concave".

A closed form expression for the density  $f(x)$  of the distribution  $S_\alpha(\sigma, \beta, \mu)$  is available in the following cases (and only in those cases):  $\alpha = 2$  (Gaussian distributions);  $\alpha = 1$  and  $\beta = 0$  (Cauchy distributions);  $\alpha = 1/2$  and  $\beta = \pm 1$  (Lévy distributions).<sup>4</sup> Degenerate distributions correspond to the limiting case  $\alpha = 0$ .

The index of stability  $\alpha$  characterizes the heaviness (the rate of decay) of the tails of stable distributions. In particular, if  $X \sim S_\alpha(\sigma, \beta, \mu)$ , then there exists a constant  $C > 0$  such that

$$P(|X| > x) \simeq \frac{C}{x^\alpha}, \quad x \rightarrow +\infty \quad (3)$$

(here and throughout the paper, we write  $g(x) \simeq h(x)$  as  $x \rightarrow x_0 \in \mathbf{R}$  or as  $x \rightarrow \infty$  if  $g(x)/h(x) \rightarrow 1$  as  $x \rightarrow x_0$  or as  $x \rightarrow \infty$ ). This implies that the  $p$ -th absolute moments  $E|X|^p$  of a r.v.  $X \sim S_\alpha(\sigma, \beta, \mu)$ ,  $\alpha \in (0, 2)$  are finite if  $p < \alpha$  and are infinite otherwise. The symmetry index  $\beta$  characterizes the skewness of the distribution. The stable distributions with  $\beta = 0$  are symmetric about the location parameter  $\mu$ . The stable distributions with  $\beta = \pm 1$  and  $\alpha \in (0, 1)$  (and only they) are one-sided, the support of these distributions is the semi-axis  $[\mu, \infty)$  for  $\beta = 1$  and is  $(-\infty, \mu]$  for  $\beta = -1$  (in particular, the Lévy distribution with  $\mu = 0$  is concentrated on the positive semi-axis  $[0, \infty)$  for  $\beta = 1$  and on the negative semi-axis  $(-\infty, 0]$  for  $\beta = -1$ ). In the case  $\alpha > 1$  the location parameter  $\mu$  is the mean of the distribution  $S_\alpha(\sigma, \beta, \mu)$ . The scale parameter  $\sigma$  is a generalization of the concept of standard deviation; it coincides with the standard deviation in the special case of Gaussian distributions ( $\alpha = 2$ ).

Distributions  $S_\alpha(\sigma, \beta, \mu)$  with  $\mu = 0$  for  $\alpha \neq 1$  and  $\beta = 0$  for  $\alpha = 1$  are called strictly stable. If  $X_i \sim S_\alpha(\sigma, \beta, \mu)$ ,  $\alpha \in (0, 2]$ ,  $i = 1, \dots, n$ , are i.i.d. strictly stable r.v.'s, then

$$n^{-1/\alpha} \sum_{i=1}^n X_i \sim S_\alpha(\sigma, \beta, \mu). \quad (4)$$

Let  $\overline{\mathcal{CS}}$  stand for the class of distributions which are convolutions of symmetric stable distributions  $S_\alpha(\sigma, 0, 0)$  with characteristic exponents  $\alpha \in (1, 2]$  and  $\sigma > 0$ .<sup>5</sup> That is,  $\overline{\mathcal{CS}}$  consists of distributions of r.v.'s  $X$  such that, for some  $k \geq 1$ ,  $X = Y_1 + \dots + Y_k$ , where  $Y_i$ ,  $i = 1, \dots, k$ , are independent r.v.'s,  $Y_i \sim S_{\alpha_i}(\sigma_i, 0, 0)$ ,  $\alpha_i \in (1, 2]$ ,  $\sigma_i > 0$ ,  $i = 1, \dots, k$ .

By  $\overline{\mathcal{CSLC}}$ , we denote the class of convolutions of distributions from the classes  $\mathcal{LC}$  and  $\overline{\mathcal{CS}}$ . That is,  $\overline{\mathcal{CSLC}}$  is the class of convolutions of symmetric distributions which are either log-concave or stable with characteristic exponents greater than one.<sup>6</sup> In other words,  $\overline{\mathcal{CSLC}}$  consists of distributions of r.v.'s  $X$  such that  $X = Y_1 + Y_2$ , where  $Y_1$  and  $Y_2$  are independent r.v.'s with distributions belonging to  $\mathcal{LC}$  or  $\overline{\mathcal{CS}}$ . The distributions of r.v.'s  $X$  in  $\overline{\mathcal{CSLC}}$  are moderately heavy-tailed in the sense that they have finite first moments:  $E|X| < \infty$ .

By  $\underline{\mathcal{CS}}$ , we denote the class of distributions which are convolutions of symmetric stable distributions  $S_\alpha(\sigma, 0, 0)$  with indices of stability  $\alpha \in (0, 1)$  and  $\sigma > 0$ .<sup>7</sup> That is,  $\underline{\mathcal{CS}}$  consists of distributions of r.v.'s

<sup>4</sup>The densities of Cauchy distributions are  $f(x) = \sigma/(\pi(\sigma^2 + (x - \mu)^2))$ . Lévy distributions have densities  $f(x) = (\sigma/(2\pi))^{1/2} \exp(-\sigma/(2x))x^{-3/2}$ ,  $x \geq 0$ ;  $f(x) = 0$ ,  $x < 0$ , where  $\sigma > 0$ , and their shifted versions.

<sup>5</sup>Here and below,  $\mathcal{CS}$  stands for ‘‘convolutions of stable’’; the overline indicates relation to stable distributions with indices of stability *greater* than the threshold value 1.

<sup>6</sup> $\overline{\mathcal{CSLC}}$  stands for ‘‘convolutions of stable and log-concave’’.

<sup>7</sup>The underline indicates relation to stable distributions with indices of stability *less* than the threshold value 1.

$X$  such that, for some  $k \geq 1$ ,  $X = Y_1 + \dots + Y_k$ , where  $Y_i$ ,  $i = 1, \dots, k$ , are independent r.v.'s,  $Y_i \sim S_{\alpha_i}(\sigma_i, 0, 0)$ ,  $\alpha_i \in (0, 1)$ ,  $\sigma_i > 0$ ,  $i = 1, \dots, k$ . The distributions of r.v.'s  $X$  from the class  $\underline{\mathcal{CS}}$  are extremely heavy-tailed in the sense that their first moments are infinite:  $E|X| = \infty$ .

Symmetric (about 0) Cauchy distributions  $S_1(\sigma, 0, 0)$  are at the dividing boundary between the classes  $\underline{\mathcal{CS}}$  and  $\overline{\mathcal{CSLC}}$ . For instance, similar to the distributions in the class  $\overline{\mathcal{CSLC}}$ , Cauchy r.v.'s  $X \sim S_1(\sigma, 0, 0)$  have finite moments of order  $p < 1$ :  $E|X|^p < \infty$ ,  $p < 1$ . In addition, similar to the distributions in  $\underline{\mathcal{CS}}$ , Cauchy r.v.'s  $X \sim S_1(\sigma, 0, 0)$  have infinite moments of order  $p \geq 1$ :  $E|X|^p = \infty$ ,  $p \geq 1$ .

Clearly, one has  $\mathcal{LC} \subset \overline{\mathcal{CSLC}}$  and  $\overline{\mathcal{CS}} \subset \overline{\mathcal{CSLC}}$ . One should also note that the class  $\overline{\mathcal{CSLC}}$  is wider than the class of (two-fold) convolutions of log-concave distributions with stable distributions  $S_\alpha(\sigma, 0, 0)$  with  $\alpha \in (1, 2]$  and  $\sigma > 0$ .

Evidently, the class  $\overline{\mathcal{CS}}$  (and, thus, the class  $\overline{\mathcal{CSLC}}$ ) contains, as a subclass, *all* symmetric stable distributions  $S_\alpha(\sigma, 0, 0)$  with  $\alpha \in (1, 2]$  and  $\sigma > 0$ . For this subclass of symmetric stable distributions, asymptotic relations (3) hold with the tail index  $\alpha \in (1, 2]$ . Similarly, the class  $\underline{\mathcal{CS}}$  contains, as a subclass, *all* symmetric stable distributions  $S_\alpha(\sigma, 0, 0)$  with  $\alpha \in (0, 1)$  and  $\sigma > 0$ . For this subclass of symmetric stable distributions, relations (3) hold with the tail index  $\alpha \in (0, 1)$ . Moderately heavy-tailed distributions with finite first moments and extremely heavy-tailed distributions with infinite means can thus be distinguished using sample moments or tail index estimators such as Hill's estimator, log-log rank-size regression or their modifications (see the reviews in Embrechts *et al.*, 1997, Beirlant *et al.*, 2004, and Gabaix and Ibragimov, 2007).

In what follows, we write  $X \sim \mathcal{LC}$  (resp.,  $X \sim \overline{\mathcal{CSLC}}$  or  $X \sim \underline{\mathcal{CS}}$ ) if the distribution of the r.v.  $X$  belongs to the class  $\mathcal{LC}$  (resp.,  $\overline{\mathcal{CSLC}}$  or  $\underline{\mathcal{CS}}$ ).

### 3 Main results

The results in Theorems 1 and 2 in this section cover both the cases of convolutions of symmetric stable distributions (the classes  $\overline{\mathcal{CSLC}}$  and  $\underline{\mathcal{CS}}$ ) and skewed stable distributions  $S_\alpha(\sigma, \beta, 0)$  where  $\beta \neq 0$ . In the case of the classes  $\overline{\mathcal{CSLC}}$  and  $\underline{\mathcal{CS}}$  of convolutions of symmetric distributions, the condition  $K > 0$  in the theorems is equivalent to the condition  $r_0 < 1/2$  for  $r_0 = P(X_0 > K)$ , and the condition  $K < 0$  is equivalent to  $r_0 > 1/2$ .

Theorem 1 implies that, for moderately heavy-tailed initial distributions of the trait  $X$  in two-period ( $t = 0, 1$ ) model (1), (2) with a finite first moment  $E|X| < \infty$ , an excess of females over males or males over females in the population of parents in the initial period  $t = 0$  leads to the same phenomena for the population of the offspring in period  $t = 1$ . This is the case, in particular, for distributions in the class  $\overline{\mathcal{CSLC}}$ . Theorem 1 generalizes the results in Karlin (1984, 1992) who obtained it for the case of two-period models (1), (2) with (extremely light-tailed) symmetric log-concave distributions of the sex-determining trait  $X$ .

**Theorem 1** *Consider two-period model (1) with the cdf's of the parental contributions given by (2).*

Let  $X_0 \sim \overline{\mathcal{CSLC}}$  or  $X_0 \sim S_\alpha(\sigma, \beta, 0)$  for some  $\sigma > 0$ ,  $\beta \in [-1, 1]$ , and  $\alpha \in (1, 2]$ . If  $K > 0$ , then

$$r_1 < 1/2. \quad (5)$$

If  $K < 0$ , then

$$r_1 > 1/2. \quad (6)$$

Theorem 2 shows that the results for two-period model (1), (2) given by Theorem 1 are reversed in the case of extremely heavy-tailed initial distributions of the trait  $X$  with infinite first moments  $E|X| = \infty$  (in particular, for the distributions in the class  $\mathcal{CS}$ ). In such settings, the sex ratio  $r_t$ ,  $t = 0, 1$ , exhibits a pattern of oscillation around the balanced sex ratio case  $r = 1/2$ , namely, an excess of females over males in the initial period  $t = 0$  leads to an excess of males over females in period  $t = 1$ , and vice versa.

**Theorem 2** Consider two-period model (1) with the cdf's of the parental contributions given by (2). Let  $X_0 \sim \mathcal{CS}$  or  $X_0 \sim S_\alpha(\sigma, \beta, 0)$  for some  $\sigma > 0$ ,  $\beta \in [-1, 1]$ , and  $\alpha \in (0, 1)$ . If  $K > 0$ , then (6) holds. If  $K < 0$ , then (5) holds.

**Remark 1** Let  $X'_0$  and  $X''_0$  be independent copies of  $X_0$ . As follows from the proof of Theorems 1 and 2, the following probabilistic identity holds for the sex ratio value  $r_1$  in period  $t = 1$ :  $r_1 = \frac{P(X'_0 + X''_0 > 2K) - r_0^2}{2r_0(1-r_0)}$ . The conclusions in Theorem 1 may be illustrated using the benchmark case of the sex-determining trait with the initial normal distribution. Let  $X_0 \sim S_2(\sigma, 0, 0)$  be a symmetric normal r.v. Suppose that  $K > 0$  and, equivalently,  $r_0 = P(X_0 > K) < 1/2$ . One has  $P(X'_0 + X''_0 > 2K) = P(X_0 > \sqrt{2}K) < P(X_0 > K) = r_0$ . Thus,  $r_1 = \frac{P(X'_0 + X''_0 > 2K) - r_0^2}{2r_0(1-r_0)} = \frac{P(X_0 > \sqrt{2}K) - r_0^2}{2r_0(1-r_0)} < \frac{r_0 - r_0^2}{2r_0(1-r_0)} = 1/2$ . Similarly, the results in Theorem 2 may be illustrated using the example of the sex-determining trait  $X_0$  with a Lévy distribution  $S_{1/2}(\sigma, 1, 0)$  with  $\alpha = 1/2$ ,  $\beta = 1$  and the density  $f(x) = (\sigma/(2\pi))^{1/2} \exp(-\sigma/(2x))x^{-3/2}$ . As discussed in Section 2, this distribution is extremely heavy-tailed with  $E|X_0|^{1/2} = \infty$  and is concentrated on the positive semi-axis  $[0, \infty)$ . Using (4) with  $\alpha = 1/2$  and  $n = 2$ , we get that  $P(X'_0 + X''_0 > 2K) = P(X_0 > K/2) > P(X_0 > K) = r_0$  for  $K > 0$ . Thus, for all  $K > 0$  and, thus, for all possible values of the sex ratio in the initial period  $r_0 = P(X_0 > K)$ , one has  $r_1 = \frac{P(X'_0 + X''_0 > 2K) - r_0^2}{2r_0(1-r_0)} = \frac{P(X_0 > K/2) - r_0^2}{2r_0(1-r_0)} > \frac{r_0 - r_0^2}{2r_0(1-r_0)} = 1/2$ . Finally, let  $X_0$  have a symmetric Cauchy distribution  $X_0 \sim S_1(\sigma, 0, 0)$  which is at the dividing boundary between the classes  $\overline{\mathcal{CSLC}}$  and  $\mathcal{CS}$  in Theorems 1 and 2. Then, using (4) with  $\alpha = 1$  and  $n = 2$ , we get that  $P(X'_0 + X''_0 > 2K) = P(X_0 > K) = r_0$  for all  $K \in \mathbf{R}$ . Thus,  $r_1 = \frac{P(X'_0 + X''_0 > 2K) - r_0^2}{2r_0(1-r_0)} = \frac{r_0 - r_0^2}{2r_0(1-r_0)} = 1/2$  for all  $K \in \mathbf{R}$ . Consequently, in the case of Cauchy distributions of  $X_0$  with  $\alpha = 1$ , the sex-ratio  $r_1$  in period  $t = 1$  stabilizes at the balanced sex-ratio value  $r_1 = 1/2$ , regardless of the values of the threshold  $K$  and the value of the sex-ratio  $r_0$  in the initial period  $t = 0$ .

Let us denote by  $d_t = |r_t - 1/2|$ ,  $t = 0, 1$ , the distances of the values of the sex-ratio among parents ( $t = 0$ ) and among the offspring ( $t = 1$ ) from the balanced sex-ratio value  $r = 1/2$  in two-period model (1), (2). Further, assuming that parents live longer than one period, we denote by  $R = (r_0 + r_1)/2$



the sex-ratio in the total population alive at time  $t = 1$ . The following theorem gives results on the magnitude of intergenerational changes in the distances  $d_t$ ,  $t = 0, 1$ , in the case of symmetric stable distributions  $S_\alpha(\sigma, 0, 0)$  of the initial trait  $X_0$ . In particular, according to the theorem, for all above distributions of  $X_0$ , the sex-ratio  $r_1$  among offspring (and, therefore, the sex-ratio in the total alive population) at  $t = 1$  becomes closer to the value  $r = 1/2$ , if the sex-ratio  $r_0$  among parents ( $t = 0$ ) is sufficiently far from it. In addition, if the distribution of  $X_0$  is symmetric stable  $S_\alpha(\sigma, 0, 0)$  with the tail index  $\alpha \in (1/2, 2]$ , then the sex ratio  $r_1$  becomes closer to the value  $r = 1/2$  also in the case if  $r_0$  is sufficiently close to it. These conclusions, however, do not hold if the distribution of the initial trait is symmetric stable  $S_\alpha(\sigma, 0, 0)$  with the tail index  $\alpha < 1/2$  and the sex-ratio value among parents  $r_0$  is sufficiently close to  $r = 1/2$ . If such patterns are present, then the oscillations in the sex-ratio  $r_t$  about the balanced sex-ratio value are increasing in the magnitude over the two generations in periods  $t = 0, 1$ . Furthermore, if the initial trait  $X_0$  has a symmetric stable distribution  $S_\alpha(\sigma, 0, 0)$  with the tail index  $\alpha < 1/2$ , then the value of the sex-ratio  $R$  in the total population in period  $t = 1$  stabilizes at the balanced sex-ratio  $R = 1/2$  for some values of the distance  $d_0$  from  $r_0$  to  $r = 1/2$ .

**Theorem 3** Consider two-period model (1) with the cdf's of the parental contributions given by (2) and the initial trait  $X_0 \sim S_\alpha(\sigma, 0, 0)$ ,  $\sigma > 0$ ,  $\alpha \in (0, 2]$ ,  $\alpha \neq 1$ . There exists  $d_0^{(1)} \in (0, 1/2)$  such that

$$d_1 < d_0 \text{ for } d_0 \geq d_0^{(1)}. \quad (7)$$

Further, if  $\alpha \in (1/2, 2]$ , then there exists  $d_0^{(2)} \in (0, 1/2)$  such that

$$d_1 < d_0, \text{ for } d_0 \leq d_0^{(2)}. \quad (8)$$

If  $\alpha \in (0, 1/2)$ , then there exist  $d_0^{(3)}, d_0^{(4)} \in (0, 1/2)$  such that

$$d_1 > d_0, \text{ for } d_0 \leq d_0^{(3)}, \quad (9)$$

$$R = 1/2 \text{ (equivalently, } d_1 = d_0) \text{ for } d_0 = d_0^{(4)}. \quad (10)$$

Theorem 4 shows that the results in Theorems 1 and 2 continue to hold for two-period models (1), (2) and bounded distributions of traits  $X_0$ , as long as these traits are concentrated on a sufficiently large interval. In what follows, we will consider  $B$ -truncations of a r.v.  $Y$  defined by  $Y^B = YI(|Y| \leq B)$ , where  $I(\cdot)$  stands for the indicator function.

**Theorem 4** Consider model (1) with the cdf's of the parental contributions given by (2) and the initial trait  $X_0^B = X_0I(|X_0| \leq B)$ , where  $B > 0$  and  $X_0$  is a real-valued r.v. Then, under their assumptions on  $X_0$ , Theorems 1 and 2 hold for a sufficiently large  $B \geq B_0$ .

**Remark 2** Using extensions of Propositions 1 and 2 in Appendix A1 to the case of dependence in Ibragimov (2005, 2007a) one can obtain, similar to the proof of the results in the paper, their generalizations to the case of parental contributions  $X_t^p, X_t^m$  with joint  $\alpha$ -symmetric distributions.<sup>8</sup>

<sup>8</sup>As discussed in Ibragimov (2007a),  $\alpha$ -symmetric distributions contain, as subclasses, models with multiplicative common shocks as well as spherical distributions. Spherical distributions, in turn, include such examples as Kotz type, multinormal, logistic and multivariate  $\alpha$ -stable distributions. In addition, they include a subclass of mixtures of normal distributions as well as multivariate  $t$ -distributions that were used in the literature to model heavy-tailedness phenomena with finite moments up to a certain order.

## 4 Concluding remarks

This paper has focused on the analysis of the sex ratio in two-period threshold sex determination models under heavy-tailedness in the framework of (possibly skewed) stable distributions and their convolutions. The results obtained imply that the sex ratio dynamics in such models depends crucially on the degree of heavy-tailedness of the sex-determining trait in the initial period. The patterns in the sex ratio dynamics over two periods are opposite for moderately heavy-tailed and extremely heavy-tailed initial distributions of the sex-determining trait.

The analysis of threshold sex determination models with heavy-tailed traits in multiperiod settings is an important open problem. Section 9.3 in Karlin and Lessard (1986) implies a sex ratio different from the balanced value  $1/2$  can evolve in the limit as  $t \rightarrow \infty$  in finite-variance analogues of models (1), (2) with environmental shocks and uniform threshold sex determination criterion. Namely, a biased limiting sex ratio appears in these models if heritability is asymmetric or the mean of the environmental shock is different from  $1/2$ . Theorem 9.2 in Section 9.4 in Karlin and Lessard (1986) further implies that the sex ratio  $r_t$  in multiperiod models (1), (2) with log-concavely distributed (and, thus, extremely light-tailed) initial traits  $X_0$  converges to the balanced value  $r = 1/2$  as  $t \rightarrow \infty$ . Extension of these results to heavy-tailed case appears to be a very difficult problem and is left for further research.<sup>9</sup>

## Appendix A1: Tail probabilities of heavy-tailed r.v.'s

This appendix summarizes the results on comparisons and the asymptotics of tail probabilities of heavy-tailed r.v.'s needed for the analysis in the paper.

Proposition 1 follows from Theorem 1.2.3 in Ibragimov (2005) (and also from part (i) of Theorem 3.1 in Ibragimov, 2007a, and its proof).

**Proposition 1** *Suppose that  $Y_1, Y_2$  are i.i.d. r.v.'s such that  $Y_1, Y_2 \sim \overline{\mathcal{CSLC}}$  or  $Y_1, Y_2 \sim S_\alpha(\sigma, \beta, 0)$  for some  $\sigma > 0$ ,  $\beta \in [-1, 1]$ , and  $\alpha \in (1, 2]$ . Then  $P(Y_1 + Y_2 > 2K) < P(Y_1 > K)$  for  $K > 0$ , and  $P(Y_1 + Y_2 > 2K) > P(Y_1 > K)$  for  $K < 0$ .*

Proposition 2 follows from Theorem 1.2.4 in Ibragimov (2005) (and also from part (i) of Theorem 3.2 in Ibragimov, 2007a, and its proof).

**Proposition 2** *Suppose that  $Y_1, Y_2$  are i.i.d. r.v.'s such that  $Y_1, Y_2 \sim \underline{\mathcal{CS}}$  or  $Y_1, Y_2 \sim S_\alpha(\sigma, \beta, 0)$  for some  $\sigma > 0$ ,  $\beta \in [-1, 1]$ , and  $\alpha \in (0, 1)$ . Then  $P(Y_1 + Y_2 > 2K) > P(Y_1 > K)$  for  $K > 0$ , and  $P(Y_1 + Y_2 > 2K) < P(Y_1 > K)$  for  $K < 0$ .*

Proposition 3 is a corollary of Propositions 1 and 2 and weak convergence properties for  $B$ -truncations:  $Y_1^B = Y_1 I(|Y_1| \leq B) \rightarrow Y_1$ ,  $Y_1^B + Y_2^B = Y_1 I(|Y_1| \leq B) + Y_2 I(|Y_2| \leq B) \rightarrow Y_1 + Y_2$  (in

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<sup>9</sup>The assumption that the initial distribution of the sex-determining trait  $X$  is log-concave implies the remarkable property that  $X_t$  in models (1), (2) is log-concavely distributed for all periods  $t \geq 1$  (see Appendix B in Karlin and Lessard, 1986). This greatly simplifies the analysis of multi-period threshold sex determination models with log-concavely distributed  $X_0$ . Similar properties do not hold for heavy-tailed distributions considered in the paper.

distribution) as  $B \rightarrow \infty$  (see Ibragimov and Walden, 2007, for extensions of the results and their applications in portfolio choice and risk management problems).

**Proposition 3** *Propositions 1 and 2 hold for  $B$ -truncations  $Y_1^B = Y_1 I(|Y_1| \leq B)$  and  $Y_2^B = Y_2 I(|Y_2| \leq B)$  with a sufficiently large  $B \geq B_0$ .*

Proposition 4 is a corollary of asymptotic expansions (2.4.3) and (2.4.4) for stable cdf's in Theorem 2.4.2 in Zolotarev (1986, p. 89). It provides an asymptotic expansion for cdf's of symmetric stable r.v.'s in the neighborhood of zero that complements asymptotic relation (3).<sup>10</sup>

**Proposition 4** *If  $X \sim S_\alpha(\sigma, 0, 0)$ ,  $\alpha \in (0, 1) \cup (1, 2]$ , then there exists a constant  $C > 0$  such that  $P(X > x) \simeq 1/2 - Cx$  as  $x \rightarrow 0$ .*

## Appendix A2: Proofs

Proof of Theorems 1 and 2. Suppose that  $X_0 \sim \mathcal{CS}$  or  $X_0 \sim S_\alpha(\sigma, \beta, 0)$  for some  $\sigma > 0$ ,  $\beta \in [-1, 1]$ , and  $\alpha \in (0, 1)$ . Let  $X_0^p$  and  $X_0^m$  be independent r.v.'s with the cdf's (2). Further, let  $r_0 = P(X_0 > K)$  be the sex-ratio in period  $t = 0$  and let  $X_0'$  and  $X_0''$  be independent copies of  $X_0$ . Define the following events:  $A_0 = \{(X_0' + X_0'')/2 > K\}$ ,  $A_1 = \{X_0' > K, X_0'' \leq K\}$ ,  $A_2 = \{X_0' \leq K, X_0'' > K\}$ ,  $A_3 = \{X_0' \leq K, X_0'' \leq K\}$  and  $A_4 = \{X_0' > K, X_0'' > K\}$ . It is not difficult to see (see Karlin, 1984, p. 263) that the sex ratio  $r_1 = P(X_1 > K)$  in period  $t = 1$  equals to

$$r_1 = P(A_0|A_1) = P(A_0 \cap A_1)/P(A_1). \quad (11)$$

It is easy to see that  $A_0 \cap A_3 = \emptyset$  and  $A_4 \subseteq A_0$ . Therefore,

$$\begin{aligned} 2P(A_0 \cap A_1) &= P(A_0 \cap A_1) + P(A_0 \cap A_2) = \\ &= \sum_{i=1}^4 P(A_0 \cap A_i) - P(A_0 \cap A_3) - P(A_0 \cap A_4) = P(A_0) - P(A_4). \end{aligned} \quad (12)$$

From independence of the r.v.'s  $X_0'$  and  $X_0''$  it follows that

$$P(A_1) = P(X_0' > K)P(X_0'' \leq K) = P(X_0 > K)(1 - P(X_0 > K)) = r_0(1 - r_0), \quad (13)$$

$$P(A_4) = P(X_0' > K)P(X_0'' > K) = r_0^2. \quad (14)$$

Using relations (11)-(14) we get

$$r_1 = (P(A_0) - P(A_4))/(2P(A_1)) = (P(A_0) - r_0^2)/(2r_0(1 - r_0)). \quad (15)$$

From Proposition 2 it follows that  $P(A_0) = P((X_0' + X_0'')/2 > K) > P(X_0 > K) = r_0$  if  $K > 0$ , and  $P(A_0) = P((X_0' + X_0'')/2 > K) < P(X_0 > K) = r_0$  if  $K < 0$ . These inequalities, together with

<sup>10</sup>Note that the second term in relation (2.4.4) in Zolotarev (1989, p. 89) should read  $-\frac{1}{2}\alpha'(1+\beta')$  instead of  $\frac{1}{2}\alpha'(1+\beta')$ ; see also the asymptotic expansions (2.4.6) and (2.5.1) for stable densities on pp. 89 and 94 in Zolotarev (1989) implied by relations (2.4.3) and (2.4.4) in the book.

(15), imply that  $r_1 > (r_0 - r_0^2)/(2r_0(1 - r_0)) = 1/2$  for  $K > 0$  and  $r_1 < (r_0 - r_0^2)/(2r_0(1 - r_0)) = 1/2$  for  $K < 0$ . Therefore, Theorem 2 holds. Let now  $X_0 \sim \overline{\mathcal{CSLC}}$  or  $X_0 \sim S_\alpha(\sigma, \beta, 0)$  for some  $\sigma > 0$ ,  $\beta \in [-1, 1]$ , and  $\alpha \in (1, 2]$ . Similar to the above, from Proposition 1 and relation (15) it follows that, for such distributions of  $X_0$ , one has  $r_1 < 1/2$  if  $K > 0$  and  $r_1 > 1/2$  if  $K < 0$ . This proves Theorem 1. ■

Proof of Theorem 3. Let  $X_0 \sim S_\alpha(\sigma, 0, 0)$ ,  $\sigma > 0$ ,  $\alpha \in (0, 1) \cup (1, 2]$ . Further, let, as in the proof of Theorems 1 and 2,  $X'_0$  and  $X''_0$  be independent copies of  $X_0$  and let  $A_0 = \{(X'_0 + X''_0)/2 > K\}$ . Since  $(X'_0 + X''_0)/2^{1/\alpha} \sim S_\alpha(\sigma, 0, 0)$  by (4) with  $n = 2$ , we have  $P(A_0) = P(X_0 > 2^{1-1/\alpha}K)$ . This, together with property (3) and Proposition 4 implies that there exist constants  $C_1, C_2 > 0$  such that  $r_0 = P(X_0 > K) \simeq C_1/K^\alpha$ ,  $P(A_0) \simeq C_1/(2^{\alpha-1}K^\alpha)$ ,  $K \rightarrow +\infty$ ;  $r_0 \simeq 1 - C_1/|K|^\alpha$ ,  $P(A_0) \simeq 1 - C_1/(2^{\alpha-1}|K|^\alpha)$ ,  $K \rightarrow -\infty$ ;  $r_0 \simeq 1/2 - C_2K$ ,  $P(A_0) \simeq 1/2 - 2^{1-1/\alpha}C_2K$ ,  $K \rightarrow 0$ . We get, therefore, that  $d_0 = |r_0 - 1/2| \simeq 1/2 - C_1/|K|^\alpha$ ,  $K \rightarrow \pm\infty$ , and  $d_0 \simeq C_2|K|$ ,  $K \rightarrow 0$ . Similarly, since, by (15),  $d_1 = |r_1 - 1/2| = |P(A_0) - r_0|/(2r_0(1 - r_0))$ , one has that  $d_1 \simeq |1/2 - 1/2^\alpha| - |1/2 - 1/2^\alpha|C_1/|K|^\alpha$ ,  $K \rightarrow \pm\infty$ , and  $d_1 \simeq C_2|(2 - 2^{2-1/\alpha})K|$ ,  $K \rightarrow 0$ . Using the above relations and the fact that  $d_0$  is increasing in  $|K|$ , it is not difficult to check that relations (7)-(9) indeed hold. Relation (10) follows from (7) and (9) and continuity of  $d_1 - d_0$  in  $K \in \mathbf{R}$ . ■

Proof of Theorem 4. The property that Theorems 1-3 hold for  $B$ -truncations  $X_0^B = X_0I(|X_0| \leq B)$  with a sufficiently large  $B \geq B_0$  follows similar to the arguments for the theorems, with the use of Proposition 3 instead of Propositions 1 and 2. ■

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