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Fisher's lost model of runaway sexual selection

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The bizarre elaboration of sexually selected traits such as the peacock's tail was a puzzle to Charles Darwin and his 19th century followers. Ronald A. Fisher crafted an ingenious solution in the 1930s, positing that female preferences would become genetically correlated with preferred traits due to nonrandom mating. These genetic correlations would translate selection for preferred traits into selection for stronger preferences, leading to a self-reinforcing process of ever-elaborating traits and preferences. It is widely believed that Fisher provided only a verbal model of this "runaway" process. However, in correspondence with Charles Galton Darwin, Fisher also laid out a simple mathematical model that purportedly confirms his verbal prediction of runaway sexual selection. Unfortunately, Fisher's model contains inconsistencies that render his quantitative conclusions inaccurate. Here, we correct Fisher's model and show that it contains all the ingredients of a working runaway process. We derive quantitative predictions of his model using numerical techniques that were unavailable in Fisher's time. Depending on parameter values, mean traits and preferences may increase until genetic variance is depleted by selection, exaggerate exponentially while their variances remain stable, or both means and variances may increase super-exponentially. We thus present the earliest mathematical model of runaway sexual selection.

KEY WORDS: Coevolution, Lande-Kirkpatrick, mechanism, quantitative genetics, Ronald A. Fisher, selection-sexual, sexy sons.

In *The Descent of Man and Selection in Relation to Sex*, Charles Darwin proposed that the elaborate ornaments of many species, borne most commonly by males, evolved due to preferences for such traits by the opposite sex (Darwin 1871). Famously, Darwin left alone the question of why such apparently extravagant preferences should evolve in the first place. Ronald A. Fisher provided a solution in his 1930 book *The Genetical Theory of Natural Selection*, expanding upon allusions in an earlier paper (Fisher 1915). If females have some modest initial preference for a particular trait, then this preference will become genetically correlated with the preferred trait. Sexual selection for males with larger trait values then indirectly favors genes for stronger preferences. This genetic association can lead to a self-reinforcing process, where both traits and preference become more extreme over evolutionary time.

It is widely believed that Fisher provided only a qualitative verbal model of the runaway process, leaving mathematical formalization to future generations of biologists (e.g., the models of O'Donald 1962, 1980; Lande 1981; Kirkpatrick 1982). For instance, Karlin (1992) refers to Fisher's "qualitative scenario" and "verbal theory," and says that "many (others) have tried to quantify Fisher's proposal." O'Donald (1990) similarly writes that 'polygenic models [of the runaway process]... were first studied by Lande in 1981'. Hoquet and Levandowsky (2015) remarked on the oddity that "Fisher, an early pioneer in the field of applied mathematical statistics, did not construct a mathematical model of the [runaway] process." More recently, Prum (2017) repeats that "Fisher never presented an explicit mathematical model of his runaway process."

Despite this widespread belief, Fisher did construct a mathematical model of the runaway process, although it was never published in his lifetime. Fisher's model was laid out in private correspondence with Charles Galton Darwin, a physicist who was also the grandson of his more famous eponymous ancestor. These letters, excerpts of which appear in Henry Bennett's variorum edition of *The Genetical Theory of Natural Selection* (Fisher 1999), were not included in earlier editions of the same book (Fisher 1930, 1958). It is consequently no surprise that their impact has not been widely felt in the field. Indeed, apart from Bennett's (1999) own discussion and a passing mention by Edwards (2011), we were unable to find any mention at all of Fisher's model in the literature.

Fisher's model predates the next mathematical treatment of the runaway process (O'Donald 1962) by 30 years and the first quantitative genetic treatment (Lande 1981) by half a century. It is consequently of great interest what his model says and to what extent it anticipates future work. Here, we dissect Fisher's model in detail. We show that, due to a pair of mathematical inconsistencies, Fisher's quantitative predictions are incorrect. Nonetheless, his correspondence contains all the necessary conceptual and mathematical ingredients for a working model of the runaway process. We correct his model and derive its predictions using numerical techniques.

In Fisher's Words

Before getting started, it is instructive to hear Fisher's model in his own words. After reading the first edition of *The Genetical Theory of Natural Selection*, C. G. Darwin had written to Fisher on July 11, 1930, saying that he was "still unconvinced" by the runaway process and asking for formal mathematical justification of Fisher's claims. Fisher replied on October 25, 1932, saying[1]:

> . . . Take x for cock beauty, and y for hen taste [NB: Fisher and Darwin discussed the runaway process via the example of mate choice in domestic fowl]. These will vary about some means $\bar{x}$ and $\bar{y}$; of which $\bar{x}$ will not matter, for there is no natural zero for this measurement, but $\bar{y}$ will, for $y = 0$ would represent indifference, and $\bar{y}$ the average intensity of preference. We may suppose for convenience that x and y are genetic values so that their averages in the offspring are the averages for the two parents, and that for each the scale of measurement is so chosen that the mean values of $(x-\bar{x})^2$ and $(y-\bar{y})^2$ are both unity. They may be correlated to a degree which must be determined from the problem so we may put r for the average value of $(x-\bar{x})(y-\bar{y})$.
>
> We might suppose beauty to be measured objectively e.g. by the length of feathers in a ruff, but taste will have to be measured by actual performance. A hen with no taste would mate at random, i.e., on the average of a number of trials, the average x of the cock she mates with is $\bar{x}$. A selective hen will lose some opportunities for mating with ugly cocks and will score a higher average. On our scale of measurement I will say that her value is y if the average beauty of the cock she chooses is $\bar{x}+ky$. k is a datum depending on powers of discrimination, opportunities for choice, etc.
>
> If a cock with specification x_1, y_1 mates with a hen specified by x_2, y_2 the offspring vary about the average $\frac{x_1+x_2}{2}, \frac{y_1+y_2}{2}$. The only hypothesis about heredity we need is that within this progeny x and y are uncorrelated; if this is true, then the mean product r in the progeny generation will be merely
>
> $$\frac{1}{4}(x_1-\bar{x}+x_2-\bar{x})(y_1-\bar{y}+y_2-\bar{y}) \qquad \text{(F1)}$$
>
> averaged over all matings. If this is the same as in the previous generation we can find r, for the average value of
>
> $$(x_1-\bar{x})\,(y_1-\bar{y}) = r \quad \text{and} \quad (x_2-\bar{x})\,(y_2-\bar{y}) = r \qquad \text{(F2)}$$
>
> while for the rest
>
> $$(x_1-\bar{x})\,(y_2-\bar{y}) = ky_2\,(y_2-\bar{y}) = k \quad \text{and}$$
> $$(x_2-\bar{x})\,(y_1-\bar{y}) = r^2\,k \qquad \text{(F3)}$$
>
> as appears from averaging the kinds of cock which any particular hen x_2, y_2 will mate with.
>
> It appears then that
>
> $$2r = k(1+r^2) \quad \text{or} \quad r = \frac{1-\sqrt{1-k^2}}{k} \qquad \text{(F4)}$$
>
> and a selection which raises the average of x by $\frac{1}{2}k\bar{y}$ in each generation must raise the average of y by $\frac{1}{2}kr\bar{y}$ i.e. $\bar{y}$ increases in geometrical progression, supposing k, and therefore r, to be constant. Of course in this I have ignored all checks, some of which may work slightly from the start, while others will certainly come in powerfully later.
>
> Let me know if I have made any headway, as I found myself entirely dissatisfied with my inability to get the argument across, and I hope the point that x and y must be correlated may remove the difficulty you feel.

Darwin replied, saying that he could not follow the derivation of $(x_2-\bar{x})\,(y_1-\bar{y}) = r^2\,k$ (eqn. F3). He also asked Fisher whether the same exponential increase could be expected in sex-limited traits that are not under sexual selection, such as milk yield. Fisher replied on November 22, 1932:

> Sorry I left the $(x_2-\bar{x})(y_1-\bar{y})$ evaluation obscure. The argument would go like this:
>
> Hens selected for or the aggregate of hens having x_2 will have taste above the average by $r(x_2-\bar{x})$. They will therefore mate with cocks above the average in beauty by $rk(x_2-\bar{x})$ and therefore with cocks above the average in taste by $r^2k(x_2-\bar{x})$. So the average of $(x_2-\bar{x})(y_1-\bar{y})$ will be the average of $r^2k\,(x_2-\bar{x})^2 = r^2\,k$. The term does not matter, and I doubted its existence for a while, but it does belong.
>
> I am sending this without answering the rest of your letter, so as to catch you with the point still in mind. Selous' observations on the Ruff, where he has seen the hen passing with perfect self composure among the crowd of males, who await, but cannot hurry, her choice, provide a perfect ecological framework for this runaway type of selection. The hens choose the fashion of their sons' ornaments.

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[1] We are grateful to the Special Collections at The University of Adelaide Library for permission to reproduce these extracts from the R. A. Fisher Digital Archive (available online at http://hdl.handle.net/2440/67635). Equation numbers have been added for clarity.

> The exponential element, which I agree is the kernel of the thing, arises from the rate of change in hen taste being proportional to the absolute average degree of taste ($\delta y \propto \bar{y}$). The milk yield is, of course transmitted through the bull, but the intensity of selection in favour of higher milk yield is not determined by the average milk yield. Again the drone bee has large eyes probably only to see the queen during the nuptial flight, and this quality selected thus in the male is transmitted presumably both to his sons, and to his daughters' sons, but the intensity of selection in no way depends on the actual average size of the eye, so there is no tendency to exponential increase.

As far as we know, this was the end of Fisher and Darwin's correspondence on runaway sexual selection, although they continued to exchange letters for many years (Fisher's correspondence with C. G. Darwin and many other individuals is available online in the University of Adelaide's R. A. Fisher Digital Archive at http://hdl.handle.net/2440/67635).

Correcting Fisher's Model

Fisher's model appears at first glance reasonable enough, but it contains two subtle inconsistencies. First, Fisher assumes that both traits x and preferences y have unit variance in the parental population. However, this normalization procedure is problematic when iterating the model over multiple generations. This is because re-normalizing female preferences each generation is a not a neutral "change of scale," but rather transforms the preference distribution away from its evolved value, thereby altering the evolutionary trajectories of both traits and preferences. This inconsistency might be seen as fairly benign. After all, similar assumptions are made in most quantitative genetic models of Fisherian sexual selection (e.g., Lande 1981; Iwasa et al. 1991), which treat the genetic variances and covariances of traits and preferences as fixed parameters (for partial relaxations of this assumption, see Barton and Turelli 1991; Pomiankowski and Iwasa 1993). Nonetheless, faithfully accounting for the evolution of preference variation yields some interesting predictions, as we shall see.

More egregious is Fisher's assumption that the covariance between traits x_1 and unexpressed preferences y_1 among mating males equals their covariance in the parental population as a whole. This assumption is represented by the first part of equation (F2). In general, however, these two covariances differ. For simplicity, suppose that a female with preference y_2 always chooses partners with trait values of *exactly* $\bar{x} + k y_2$ (we relax this assumption in the Supporting Information). For ease of comparison, let us also retain Fisher's assumption that $\sigma_x^2 = \sigma_y^2 = 1$. In this case, the covariance between traits and preferences in the parental population is $\sigma_{xy} = r$, whereas the covariance among mating males is $\sigma_{x_1 y_1} = k^2 r$ (for details, see Methods section). The intuition that these values must differ is most easily obtained when $k = 0$. In this case, all females choose males with trait values that are exactly average. There is consequently no variance in male trait values, and so the covariance $\sigma_{x_1 y_1} = 0$.

As a consequence of these two inconsistencies, the equilibrium condition derived in equation (F4) is incorrect. Below, we reconstruct and correct Fisher's model. Doing so requires three additional assumptions that are not explicit in the original model. First, we must specify a joint distribution of traits and preferences in the parental generation. In fact, Fisher's original argument does not hold for arbitrary joint distributions, but only those where individuals with trait values of $\bar{x} + \Delta$ have preference values of $\bar{y} + \Delta r$ on average, regardless of the value of Δ. We will assume that traits and preferences in the parental generation follow a bivariate normal distribution. Second, we require a more concrete specification of female choice. For simplicity, we assume that if a female has preference y_2, her mates have trait values that are exactly $k y_2$ standard deviations above the mean (i.e., there is no variance around the average in Fisher's model). We relax this assumption in the Supporting Information, where we allow for errors in female mate choice. Third, we allow for the variance in traits and preferences to be renewed each generation by meiosis and mutation. Without such variational input, the variance in these characters would quickly be depleted in the absence of strongly disruptive or temporally variable selection.

Methods

Following Fisher, we distinguish among trait and preference values in three contexts: in the parental generation before mating occurs (x and y), among mating males (x_1 and y_1) and among mating females (x_2 and y_2). We assume that these values are entirely genetically determined (i.e., with no environmental contribution). We also suppose that (x, y) initially follows a bivariate normal distribution (which is implicit in Fisher's argument). Fisher assumes that x and y have unit variance in the parental generation, with the consequence that the covariance and the correlation between these traits coincide. In contrast, we normalize neither traits nor preferences. We write σ_x^2 and σ_y^2 for their variances, σ_{xy} for their covariance, and $r = \frac{\sigma_{xy}}{\sigma_x \sigma_y}$ for their correlation.

We will first calculate the variance–covariance matrix for the traits (x_1, y_1, x_2, y_2) among mating pairs. By assumption, neither trait nor preference is under direct selection in females, and so their joint distribution (x_2, y_2) among mating females equals their distribution (x, y) in the parental generation. This means that $\sigma_{x_2}^2 = \sigma_x^2$, $\sigma_{y_2}^2 = \sigma_y^2$, and $\sigma_{x_2 y_2} = \sigma_{xy}$. In contrast, females' non-random choice of mates transforms the trait-preference distribution (x_1, y_1) of mating males. Fisher assumes that if a female has mating trait y_2, then her mates' trait values are on average $k y_2$ standard deviations above the mean. For non-normalized trait values, this average is given by $\bar{x} + k\sigma_x y_2$. For simplicity, we assume that females always mate with males of exactly this trait value (we relax this assumption in the Supporting Information). The trait values of mating males are represented by the random variable $x_1 = \bar{x} \ + k\sigma_x y_2$, where y_2 represents the trait values of mating females. The variance in mating males' trait values is:

$$\sigma_{x_1}^2 = k^2\, \sigma_x^2 \sigma_y^2 \tag{1}$$

By assumption, traits and preferences are bivariate normal in the parental population and preference values are selectively neutral in males. The distribution of preference values y_1 among males with trait value x_1 is then normal with mean $\mathbb{E}\,(y_1|x_1) = \bar{y} \ + r\frac{\sigma_y}{\sigma_x}(x_1 - \bar{x})$ and variance $(1 - r^2)\sigma_y^2$ (see, e.g., Kotz et al. 2000). Using equation (1) and the law of total variance, the variance in preference values among mating males is then:

$$\begin{aligned} \sigma_{y_1}^2 &= \mathbb{E}\,(\mathrm{var}\,(y_1|x_1)) + \mathrm{var}\,(\mathbb{E}\,(y_1|x_1)) \\ &= \sigma_y^2 \left(1 + r^2 \left(k^2\sigma_y^2 - 1\right)\right) \end{aligned} \tag{2}$$

Similarly, the covariance between trait and preference values among mating males is:

$$\sigma_{x_1 y_1} = \ \mathrm{cov}\,(x_1, \mathbb{E}\,(y_1|x_1)) = k^2\, r\sigma_x\sigma_y^3 \tag{3}$$

In particular, note that when $\sigma_x = \sigma_y = 1$, we have $\sigma_{x_1 y_1} = k^2\, r$, which differs from Fisher's value of r in equation (F2) (see above).

We now calculate the cross-sex covariances between males and females of a mating pair. The simplest case is the covariance between female preferences and male traits, which is just:

$$\sigma_{x_1 y_2} = \ \mathrm{cov}\,(\bar{x} + k\sigma_x y_2,\, y_2) = \ k\sigma_x\sigma_y^2 \tag{4}$$

Next, we consider the covariance between male and female trait values. Since $x_1 = \bar{x} \ + k\sigma_x y_2$ and $\sigma_{x_2 y_2} = \ r\sigma_x\sigma_y$, we have:

$$\sigma_{x_1 x_2} = \ \mathrm{cov}\,(\bar{x} + k\sigma_x y_2,\, x_2) = \ kr\sigma_x^2\sigma_y \tag{5}$$

Similarly, using equation (3) and the relationship $y_2 = \frac{1}{k\sigma_x}(x_1 - \bar{x})$, the covariance between male and female preference values is:

$$\sigma_{y_1 y_2} = \ \mathrm{cov}\left(y_1,\, \frac{1}{k\sigma_x}\,(x_1 - \bar{x})\right) = \ kr\sigma_y^3 \tag{6}$$

Lastly, by bivariate normality, we have $x_2 = \bar{x} + r\frac{\sigma_x}{\sigma_y}(y_2 - \bar{y}) + \varepsilon$, where ε is an error term that is independent of y_2, and by extension of y_1. Hence, using equation (6), the covariance between male preference values and female trait values is:

$$\sigma_{y_1 x_2} = \ \mathrm{cov}\left(y_1, \bar{x} + r\frac{\sigma_x}{\sigma_y}\,(y_2 - \bar{y}) + \varepsilon\right) = kr^2\sigma_x\sigma_y^2 \tag{7}$$

We can now derive the distribution of the midparent values of mating pairs, which are given by $x_m = \frac{x_1+x_2}{2}$ and $y_m = \frac{y_1+y_2}{2}$. These are bivariate normal with means:

$$\bar{x}_m = \bar{x} \ + \frac{1}{2}k\sigma_x\bar{y} \quad \text{and} \quad \bar{y}_m = \bar{y} \ + \frac{1}{2}kr\sigma_y\bar{y}, \tag{8}$$

variances:

$$\begin{aligned} \sigma_{x_m}^2 &= \frac{1}{4}\left(\sigma_{x_1}^2 + 2\sigma_{x_1 x_2} + \sigma_{x_2}^2\right) = \frac{1}{4}\,\sigma_x^2\left(1 + 2kr\sigma_y + k^2\sigma_y^2\right) \\ \sigma_{y_m}^2 &= \frac{1}{4}\left(\sigma_{y_1}^2 + 2\sigma_{y_1 y_2} + \sigma_{y_m}^2\right) \\ &= \ \frac{1}{4}\,\sigma_y^2\left(2 + 2kr\sigma_y + r^2\left(k^2\sigma_y^2 - 1\right)\right), \end{aligned} \tag{9}$$

and covariance:

$$\begin{aligned} \sigma_{x_m, y_m} &= \frac{1}{4}\left(\sigma_{x_1 y_1} + \sigma_{x_1 y_2} + \sigma_{x_2 y_1} + \sigma_{x_2 y_2}\right) \\ &= \frac{1}{4}\,\sigma_x\sigma_y\left(r + k^2 r\sigma_y^2 + k\sigma_y + kr^2\sigma_y\right) \end{aligned} \tag{10}$$

Let us follow the standard assumption of the infinitesimal model that the trait and preference values of the offspring of a given pair are normally distributed, with means equal to the midparent values and fixed variances that are independent of these values (Barton et al. 2017). Individual trait and preferences values in the offspring generation are then given by:

$$\left(x', y'\right) = (x_m, y_m) \ + \xi, \tag{11}$$

where ξ is normally distributed with mean zero and covariance matrix $\Sigma \ = [\begin{smallmatrix} \sigma_{\xi_x}^2 & 0 \\ 0 & \sigma_{\xi_y}^2 \end{smallmatrix}]$. The parameters $\sigma_{\xi_x}^2$ and $\sigma_{\xi_y}^2$ represent variance in the offspring generation that arises from meiosis or mutation. Note that we assume that these processes have uncorrelated effects on traits and preferences, so that the correlation r arises strictly via nonrandom mating. Under these assumptions, traits and preferences in the offspring generation are normally distributed, with means equal to the midparent means in equation (8), and variances and covariance given by:

$$\begin{aligned} \sigma_{x'}^2 &= \sigma_{x_m}^2 \ + \sigma_{\xi_x}^2 \\ \sigma_{y'}^2 &= \sigma_{x_m}^2 \ + \sigma_{\xi_x}^2 \\ \sigma_{x', y'} &= \sigma_{x_m, y_m} \end{aligned} \tag{12}$$

Given values for the parameters k, σ_{ξ_x} and σ_{ξ_y}, and initial values for $\bar{x}$, $\bar{y}$, σ_x, σ_y, and r, we can iterate the above model numerically to derive the evolutionary trajectory of trait and preference means, variances, and correlations across generations. For some values of k, σ_{ξ_x} and σ_{ξ_y} there is a trajectory where the variances σ_x^2 and σ_y^2 and the covariance σ_{xy} are stable across generations. We located such equilibria "equilibria" by setting the expressions in equation (12) equal to their values in the previous generation and solving numerically.

Results

Our corrected model predicts the occurrence of three qualitatively different outcomes (Fig. 1; note that the scales on both the horizontal and vertical axes differ among panels):

CLASSIC RUNAWAY

In this case, the mean values of traits and preferences increase without bound, while their variances and correlation approach a stable equilibrium.[2] This occurs when (1) the parameter k, the initial variance in preferences, and the variational input to preferences $\sigma^2_{\xi_y}$ are all not too large, (2) traits and preferences receive new variational input each generation (i.e., $\sigma^2_{\xi_x}, \sigma^2_{\xi_y} > 0$), and (3) the initial mean preference is non-zero. At this pseudo-equilibrium, preferences increase geometrically by a fixed proportion of $\frac{1}{2}kr\sigma_y$ each generation, just as Fisher predicted. Both the correlation r and the proportional rate of increase at equilibrium are increasing functions of k (Fig. 2). Although the equilibrium is stable, it is not a global attractor.

EXPLOSIVE RUNAWAY

The second case occurs when either the initial variance or the variational input of preferences is large. In this case, both the means and variances in traits and preferences increase super-exponentially, quickly reaching absurd values. It is notable that such explosive behavior can occur even if there is no new variational input: in this case, selection is so strong that extreme outliers in the original distributions are strongly favored, leading to a rapid increase in variance. Such outliers are always available to selection, because this quantitative genetic model implicitly assumes an infinite population size and an infinite number of loci of infinitesimal effect (Barton et al. 2017).

FIZZLE AWAY

Lastly, if there is no variational input (i.e., $\sigma^2_{\xi_x} = \sigma^2_{\xi_y} = 0$) and the initial variance in preferences is low, then sexual selection "fizzles away." Variation in both traits and preferences converges to zero, and the means of both traits and preferences plateau after an initial period of increase. If, alternatively, there is variational input to traits but not preferences ($\sigma^2_{\xi_x} > 0$ and $\sigma^2_{\xi_y} = 0$), then preferences will plateau while traits increase indefinitely (data not shown).

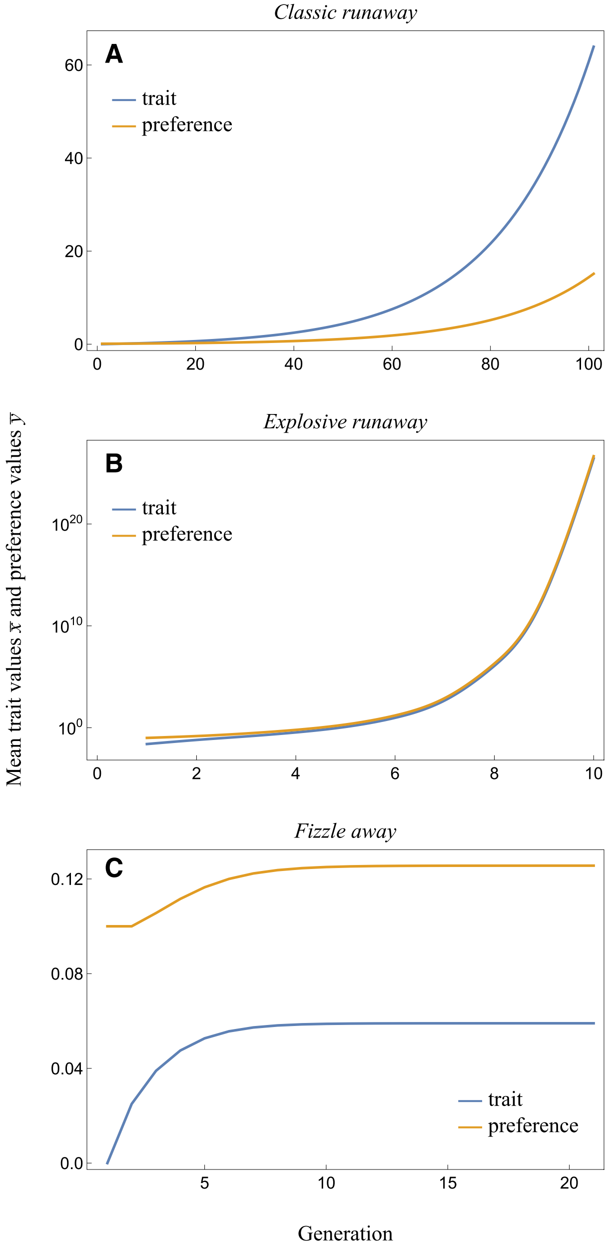

Figure 1. Coevolution of mean trait values (blue) and preference values (yellow) under three different scenarios. Note that, due to the vast differences in trait evolution among these scenarios, the scales on both the horizontal and vertical axes differ among panels. (A) *Classic runaway*, where mean traits and preferences increase according to a geometric progression. Variances in traits and preferences and the correlation between them remain constant at a stable pseudo-equilibrium. Shown with $\sigma_y = 1$ and $\sigma^2_{\xi x} = \sigma^2_{\xi y} = \frac{1}{2}$. (B) *Explosive runaway*, where the means and variances of traits and preferences increase super-exponentially. Shown with $\sigma_y = 5$ and $\sigma^2_{\xi x} = \sigma^2_{\xi y} = \frac{1}{2}$. (C) *Fizzle away*, where variance in traits and preferences is depleted. Mean traits and preferences initially rise and then plateau. Show with $\sigma_y = 1$ and $\sigma^2_{\xi x} = \sigma^2_{\xi y} = 0$. All panels are shown with $k = 0.5$, initial parameters $\bar{x} = 0$, $\bar{y} = 0.1$, $r = 0$, $\sigma_x = 1$, and other parameters as noted above.

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[2] For some parameter combinations, there is additionally an unstable equilibrium in which traits and preferences are very highly correlated (cf. Karlin and Raper 1990)

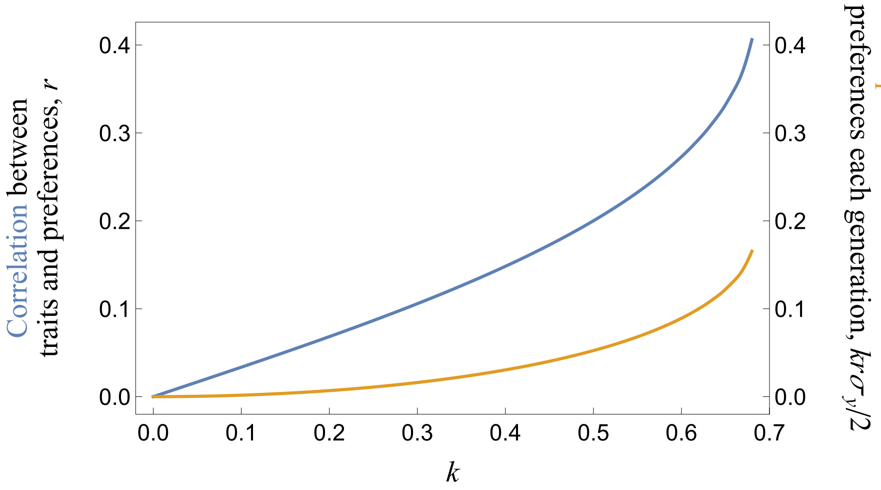

Figure 2. **Within-individual correlation r between trait and preference values (blue) and the proportional increase in mean preferences each generation (yellow) at equilibrium in the "classic runaway" scenario. The variances σ_x^2 and σ_y^2 in traits and preferences and the correlation r are stable across generations. Shown with variational inputs of $\sigma_{\xi_x}^2 = \sigma_{\xi_y}^2 = \frac{1}{2}$. When $k > 0.69$, there is no stable equilibrium for these parameter values and explosive runaway occurs (see Fig. 2).**

Our main model assumes that mate choice is perfect, in the sense that females always choose males with trait values exactly matching their preferences. Suppose, on the other hand, that realized mate choice is noisy, such that the difference between a female's preference and her mate's trait value can be represented by a normally distributed "error." Such noise introduces an additional source of variation in the trait values (and, by extension, preferences values) of mating males. This acts to maintain variation in both characters, and consequently has similar evolutionary implications to variational input via mutation (see Fig. S1).

Discussion

We have corrected Fisher's unpublished model of 1932 to produce, posthumously, the first mathematical model of runaway sexual selection. Despite a pair of mathematical inconsistencies, Fisher's letters contain all of the necessary ingredients of a working runaway process. The corrected model is more complex than Fisher's analytic sketch, and our analysis of it relies partly on numerical techniques that were unavailable in Fisher's time. Nonetheless, the corrected model is very close to the conceptual spirit of both Fisher's sketch and the verbal model in *The Genetical Theory of Natural Selection*. Among modern models, the corrected model is closest to that of Karlin and Raper (1990), which, however, contains additional elements such as viability selection on male traits.

An obvious question is why Fisher never published a formal model of runaway sexual selection, and here we can only speculate. First, it is worth noting that the situation is hardly unique. Fisher often favored verbal over mathematical models in an attempt to reach a wider audience (Edwards 2011), and many verbal models in *The Genetical Theory of Natural Selection* were never formalized by Fisher himself. Perhaps Fisher thought that his verbal model was clear enough, and eschewed the dirty and detailed work of giving it specific form. On the other hand, there is a hint of frustration at the end of Fisher's letter, where he pronounces himself "entirely dissatisfied with my inability to get the argument across." Maybe Fisher never derived a mathematical model that met his high standards. Notably, many later models of the runaway process (Lande 1981; Pomiankowski et al. 1991; Iwasa and Pomiankowski 1995; Day 2000; Kokko et al. 2015) and of sexual selection more generally (Grafen 1990; Iwasa et al. 1991; Tazzyman et al. 2014; Dhole et al. 2018: reviewed in Kuijper et al. 2012) are characterized by considerable analytical sophistication and by numerical techniques that were unavailable or impractical in Fisher's pre-digital era.

In contrast to most later work, Fisher's model contains no fitness costs or evolutionary constraints that would curb the evolution of elaborate traits. Indeed, he "ignored all checks, some of which may work slightly from the start, while others will certainly come in powerfully later." As a consequence, runaway evolution occurs very easily in this model. Indeed, a "classic" runaway is possible whenever initial female preference differs from zero on average and there is some variational input to both traits and preferences. Moreover, high initial variance in female preference can lead to an "explosive" runaway, where both the means and variances of traits and preferences increase super-exponentially.

It is amusing to imagine a peacock's tail the size of the universe, but in reality, of course, such elaboration will be dampened in multiple ways. First, there will be natural selection favoring smaller trait values (Lande 1981; Kirkpatrick 1982; Karlin and Raper 1990), which will likely increase in intensity as elaborate traits begin straining the limits of resource acquisition (Fromhage and Jennions 2016; Henshaw et al. 2019). Second, extreme female preferences will be selected against if they prevent females from finding a mate (de Jong and Sabelis 1991; Kokko and Mappes 2005; Priklopil et al. 2015; Dechaume-Moncharmont et al. 2016; Henshaw 2018). Third, strong selection for ever-elaborating traits will deplete genetic variance for those traits in finite populations (Borgia 1979; Kirkpatrick and Ryan 1991; Rowe and Houle 1996; Kotiaho et al. 2008). If traits already commandeer a large share of available resources, then presumably few mutations will arise that increase trait size while maintaining general viability. The combination of no-cost traits and unbounded genetic variability in Fisher's model enables the "explosive" runaway that would be impossible in a model with either realistic fitness trade-offs or a finite population or genetic structure.

Fisher's model was never intended to be realistic. Nonetheless, it clearly demonstrates the conceptual operation of the runaway process and would have provided an admirable formal basis for further work, had anyone known about it.

AUTHOR CONTRIBUTIONS

J.M.H. designed the model. J.M.H. and A.G.J. wrote the manuscript.

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LITERATURE CITED

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Coevolution of mean trait values (blue) and preference values (yellow) when females choose their mates with a normally distributed error with variance $\sigma_\varepsilon^2 = 0.5$.