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A Guide to Sexual Selection Theory
Kuijper, Pen, and Weissing

Supplemental Text: Four Implementations of the Fisher Process

A Population Genetics Model of the Fisher Process

Genetic assumptions. The model of Kirkpatrick (1982) works with two haploid diallelic loci, of which P is the preference locus, with alleles P_0 (no preference) and P_1 (preference for ornamented males) and T the ornament locus, with alleles T_0 (no ornamentation) and T_1 (ornamentation). The evolutionary dynamics can be described by keeping track of the changes of the relative frequencies x_{ij} of the haploid genotypes ('haplotypes') P_iT_j. It is often more convenient to describe the dynamics in terms of allele frequencies, that is the frequencies $p = x_{10} + x_{11}$ of the preference allele P_1 and $t = x_{01} + x_{11}$ of the ornament allele T_1. For a complete description, one also has to keep track of linkage disequilibrium $D = x_{00}x_{11} - x_{01}x_{10}$. In fact, the four haplotype frequencies x_{ij} can be recovered from p, t and D. In statistical terms, linkage disequilibrium corresponds to the covariance of the alleles with identical subscripts: D is positive if P_1 and T_1 or P_0 and T_0 co-occur more often in the same individual than to be expected on basis of the allele frequencies p and t. The build-up of a positive association between P_1 and T_1 (a positive D) is *the* key ingredient of the Fisher process. To derive the evolutionary dynamics of p, t and D, we closely follow Bulmer (1989).

Viability selection. The costs of expressing an ornament are assumed to be incurred during a period of viability selection, which precedes the mating stage. Ornamented males have a relative survival probability of $v_1 = 1 - s$ $(0 < s < 1)$ in comparison to the viability $v_0 = 1$ of males without ornamentation. Since ornaments are sex-limited, only males incur costs (see Seger & Trivers 1986, Albert & Otto 2005, where this assumption is relaxed). Costs of female preference are not considered in Kirpatrick's (1982) model. Viability selection changes the frequency of ornamented males from t to $t_m = t \cdot v_1 / \overline{v}$, where $\overline{v} = (1-t)v_0 + tv_1 = 1 - st$ is the mean viability of males.

Mating stage. We define U_{ij} as the probability that a female with allele P_i mates with a male carrying allele T_j. P_0 females mate at random, so that the probability of mating with T_0 and T_1 males is identical to their respective frequency in the population, $U_{00} = 1 - t_m$ and $U_{01} = t_m$. In contrast, for females carrying the P_1 allele the odds are $a > 1$ that she prefers a T_1 male over a T_0 male, so that $U_{11} : U_{10} = at_m : (1-t_m)$. This way of exerting mate choice is known as 'fixed relative preferences.' It corresponds, for example, to a situation where females encounter males one at a time in a random sequence, until they accept a male for mating (Maynard Smith 1985). Other mechanisms of mate choice can lead to very different outcomes (e.g., the 'best-of-*N*' model, Seger 1985, or the 'absolute preference' model, Takahasi 1997). Kirpatrick's model also assumes that all choosy females will eventually mate ($U_{11} + U_{10} = 1$). Together with the above condition on $U_{11} : U_{10}$ this yields $U_{10} = (1-t_m)/(1-t_m+at_m)$ and $U_{11} = at_m/(1-t_m+at_m)$.

Evolutionary dynamics. Once the frequency distribution of the various types of mating are known, the distribution of offspring genotypes can be derived in a standard way (taking into account recombination and Mendelian segregation). As shown in Bulmer (1989), this leads to the following system of difference equations describing how the allele frequencies *p* and *t* and the linkage disequilibrium *D* change from one generation to the next:

$$\begin{aligned}\Delta t &= \tfrac{1}{2} t(1-t)A \\ \Delta p &= \tfrac{1}{2} DA \\ \Delta D &= D\left((1-r)A(\tfrac{1}{2}-t) - \tfrac{1}{4}A^2 t(1-t) - r\right) + \tfrac{1}{2} rB\left(D^2 + p(1-p)t(1-t)\right)\end{aligned} \tag{A1}$$

where *r* is the recombination rate between the trait and the preference locus and *A* and *B* are defined as:

$$A = \frac{p(U_{11}-U_{01}) - (t-t_m)}{t(1-t)}, \quad B = \frac{U_{11}-U_{01}}{t(1-t)}. \tag{A2}$$

The factor $\frac{1}{2}$ in the first two equations of (A1) reflects the fact that preference and ornament are only expressed in one sex. The first equation of (A1) shows that there is direct selection on the ornament, which is characterized by the term A. This term includes two parts, corresponding to the mating advantage $p(U_{11} - U_{01})$ of ornamented males and the decline $t - t_m$ in ornament frequency in males due to natural selection. The second equation of (A1) shows that the preference allele changes in frequency as a correlated response to selection on the ornament allele: once there is a positive linkage disequilibrium D, p changes in the same direction as t. Hence, (A1) captures the essential features of the Fisher process.

Equilibria. Solving for the equilibria by setting $\Delta t = 0$ and $\Delta p = 0$, one finds a set of boundary equilibria that constitute either loss of the ornament (t=0), or fixation of the ornament (t=1). Internal equilibria have to satisfy $A = 0$. A straightforward calculation yields:

$$A = pB - \frac{s}{1-st}, \quad B = \frac{1-s}{1-st} \cdot \frac{a-1}{1-t+a(1-s)t} \tag{A3}$$

This implies that the equation $A = 0$ is equivalent to

$$p = s\frac{1+(a(1-s)-1)t}{(1-s)(a-1)} \tag{A4}$$

and that the internal equilibria constitute a line with a slope determined by the interplay of natural and sexual selection. For a given combination (p,t) on this line of equilibria, the equilibrium value of D can be obtained by solving $\Delta D = 0$, a quadratic equation in D. Since $A = 0$, this equation can be simplified considerably. It turns out that the solution of $\Delta D = 0$ does not depend on the recombination rate r. In other words, at equilibrium the statistical association between preference and ornament alleles does not depend on physical linkage.

Figure 2*a* in the main text depicts the line of equilibria and the dynamic behavior of Kirkpatrick's model. As predicted by Fisher (1915) the preference allele P_1 has to be sufficiently common initially to give rise to nonzero frequencies of the ornament allele T_1 (although this depends on the preference function, Takahashi 1997). Once P_1 is sufficiently common it either gives rise to polymorphism in which both T_0 and T_1 alleles coexist or to fixation of the T_1 allele. Notice that the approach to the set of equilibria is roughly linear. The slope of the 'lines of approach' is affected by the 'genetic' parameter r. In contrast, the line of equilibria itself only depends on the 'fitness' parameters s and a.

Costly preferences. As already noted by Kirkpatrick (1982) and further investigated by Pomiankowski (1987) and Bulmer (1989), the line of equilibria in Figure 2*a* is extremely sensitive to small deviations in the model assumptions. For example, the addition of the slightest costs of a female preference leads to a breakdown of the line of equilibria to a single equilibrium point in which mate choice is absent ($p = 0, t = 0$). Additional assumptions (like mutation bias) are then needed to explain the evolution of costly ornaments and preferences (see Figure 3 in the main text).

A quantitative genetics model of the Fisher process

Lande's (1981) quantitative genetics implementation of the Fisher process assumes that the female preference p and the male ornament t are continuous, normally distributed characters.

Viability selection. As in the population genetics model considered above, the costs of expressing an ornament are assumed to be incurred during a period of viability selection. The survival probability $v(t)$ of a male carrying an ornament t is given by a Gaussian function

$$v(t) = \exp\left[-\tfrac{1}{2}\left(\frac{t-\theta}{\omega}\right)^2\right]. \tag{A5}$$

Hence selection is stabilizing, and each deviation from the optimal ornament value θ (with respect to viability selection) leads to a decrease in survival. The smaller the term ω the stronger deviations from θ are punished by natural selection. Hence $1/\omega$ reflects the strength of viability selection against exaggerated ornaments. Exponential fitness functions like the Gaussian above are popular in quantitative genetics models, since the distribution of traits (here: male ornaments) after selection is again normal. Like Kirkpatrick’s model, Lande’s model does not consider costs of female choosiness.

Mating stage. The female “preference” is any character leading to non-random mating with respect to the male ornament. The tendency of a female with preference p to mate with an adult male with ornament value t is given by a preference function $\psi(t \mid p)$. Lande (1981) discusses three different preference functions, but here we focus on one of them: $\psi(t \mid p) = \exp(apt)$. In this ‘psychophysical model,’ females with $p \neq 0$ always prefer the most extreme males most; the sign of p determines the direction of the preference and the magnitude of p determines how strongly a female discriminates between males differing in ornamentation.

Evolutionary dynamics. It is one of the basic insights of quantitative genetics theory that the evolution of the mean values of two sex-limited traits in a population with discrete, non-overlapping generations can be described by the ‘multivariate breeder's equation’ (Lande &

Arnold 1983). There are various version of this equation that differ in their description of selection and their assumptions on the multivariate distribution of traits (Walsh & Lynch 2012). Here we follow the approach of Pomiankowski et al. (1991) that is relatively broadly applicable in case of weak selection:

$$\begin{pmatrix} \Delta\bar{t} \\ \Delta\bar{p} \end{pmatrix} = \frac{1}{2}\cdot\begin{pmatrix} G_t & G_{tp} \\ G_{tp} & G_p \end{pmatrix}\begin{pmatrix} \partial\ln(W_m)/\partial t \\ \partial\ln(W_f)/\partial p \end{pmatrix}\Bigg|_{\substack{t=\bar{t} \\ p=\bar{p}}} \tag{A6}$$

The matrix in (A6) is the so-called G-matrix, consisting of the additive genetic variances G_t and G_p of male traits and female preferences and the additive genetic covariance G_{tp} describing the (additive) genetic association between trait and preference. The vector to the right is the gradient vector of (relative) individual fitness (male fitness W_m and female fitness W_f) with respect to the individual trait values. The factor $\frac{1}{2}$ reflects the sex-limited expression of traits and preferences.

In Lande's model, the net effect of viability selection and mating preferences on the ornament trait is given by

$$\frac{\partial\ln(W_m)}{\partial t}\Bigg|_{\substack{t=\bar{t} \\ p=\bar{p}}} = a\bar{p} - \frac{\bar{t}-\theta}{\omega^2}. \tag{A7}$$

In the absence of direct selection on female preferences (no costs of choosiness), $\partial\ln(W_f)/\partial p = 0$, and (A6) can be written as

$$\begin{aligned} \Delta\bar{t} &= \tfrac{1}{2}G_t\left(a\bar{p} - \frac{\bar{t}-\theta}{\omega^2}\right) \\ \Delta\bar{p} &= \tfrac{1}{2}G_{tp}\left(a\bar{p} - \frac{\bar{t}-\theta}{\omega^2}\right) \end{aligned} \tag{A8}$$

Comparing (A8) with (A1) shows a close correspondence between Kirkpatrick's and Lande's model. If we assign the numerical values 0 and 1 to the alleles P_0 and P_1 and to T_0 and T_1 in Kirkpatrick's model, the allele frequencies *p* and *t* in this model correspond to the averages $\bar{p}$ and $\bar{t}$ of these numerical values; the term $t(1-t)$ in the first equation of (A1) corresponds to the variance (G_t) in *t*-values; and the linkage disequilibrium *D* corresponds to the covariance (G_{tp})

between p- and t-values. Finally, the term A in (A1) corresponds to $\partial \ln(W_m)/\partial t$ in Lande's model.

Equilibria. The equilibria of Lande's model ($\Delta\overline{t} = \Delta\overline{p} = 0$) are given by

$$\overline{p} = \frac{\overline{t} - \theta}{a\omega^2}. \tag{A9}$$

Hence when plotting the mean preference $\overline{p}$ against the mean trait value $\overline{t}$ a line of equilibria results with slope $1/a\omega^2$ (see Figure 2*b* in the main text). If G_t and G_{tp} are constant, the evolutionary trajectories are straight lines with slope

$$b_{pt} = \frac{\Delta\overline{p}}{\Delta\overline{t}} = \frac{G_{tp}}{G_t}, \tag{A10}$$

corresponding to the (additive) genetic regression coefficient of the preference on the trait. If this regression is weak (more precisely: if the regression line is less steep than line of equilibria, or $G_{tp}/G_t < 1/a\omega^2$), then evolution will proceed towards the line of equilibria (as in Figure 2*b* of the main text). If the genetic regression is strong, any positive selection on t quickly increases the level of p as well. In this case a self-reinforcing runaway process occurs and evolution will proceed away from the line of equilibria.

Costly preferences. Any costs of female preferences will strongly change the dynamics of Lande's model. The line of equilibria collapses to a single equilibrium point, located at the values maximizing male and female survival (i.e., $\overline{p} = \theta_p$, $\overline{t} = \theta_t$). As in S1, additional assumptions (like mutation bias) are needed to explain the evolution of costly ornaments and preferences (see Figure 3 in the main text).

An Adaptive Dynamics Model of the Fisher Process

Over the years several sexual selection models have been developed that make use of evolutionary game theory or adaptive dynamics (Pen & Weissing 2000, Kokko et al. 2002, McNamara et al. 2003, Fawcett et al. 2011). All these models have in common that they consider the invasion prospects of a rare mutant phenotype in an otherwise monomorphic ‘resident’ population.

Here, we discuss Pen &Weissing’s (2000) model for the Fisher process. This model considers a class-structured population consisting of females and two types of male: non-ornamented males (♂$_0$) and males expressing an ornament (♂$_1$). Evolvable traits are the females’ preference p for mating with ornamented males and the tendency t of a male to develop the ornament, that is, the probability to develop into a male of type 1. The aim is to find evolutionarily stable values p^* and t^* that cannot be invaded by any mutant phenotypes.

Viability selection. The survival probability of ornamented males is reduced by a factor $1-s$ when compared to non-ornamented males. Males that express an ornament survive with probability 1-c, whereas males without an ornament survive with probability 1. Costs of female preferences are not considered in Pen & Weissing’s model but included in later extensions (Fawcett et al 2011).

Mating stage. Females have a certain preference p for type 1 males, which translates into them giving a proportion α of their matings to type 1 males, $\alpha = \alpha(p)$ being an increasing function of p. For mutants and residents alike, the number of matings per type of male depends on the preference p^* of the females and on the relative frequency of the two types of (adult) males in the resident population. This follows from the assumption that mutant females and males are rare. Let u_f^*, u_{m0}^* and u_{m1}^* denote the density of females, type 0 males and type 1 males in the resident population, respectively. Then the per capita number of matings per type of male, Q_0^* and Q_1^*, can be derived from the consistency requirements $Q_0^* u_{m0}^* = (1-\alpha^*) u_f^*$ and $Q_1^* u_{m1}^* = \alpha^* u_f^*$, where $\alpha^* = \alpha(p^*)$:

$$Q_0^* = \frac{(1-\alpha^*)u_f^*}{u_{m0}^*}, \quad Q_1^* = \frac{\alpha^* u_f^*}{u_{m1}^*}. \tag{A11}$$

Stage-transition matrix. Assuming non-overlapping generations and a stationary resident population producing an even primary sex ratio (i.e., each female producing on average one male and one female offspring), the transitions between the different classes of mutant individuals from one generation to the next are summarized by the stage-transition matrix

$$\mathbf{A}\left(p,t \middle| p^*,t^*\right) = \frac{1}{2} \cdot \begin{bmatrix} 1 & Q_0^* & Q_1^* \\ 1-t & (1-t)Q_0^* & (1-t)Q_1^* \\ (1-s)t & (1-s)tQ_0^* & (1-s)tQ_1^* \end{bmatrix}. \tag{A12}$$

This matrix should be interpreted as follows. The first column characterizes the per capita contribution of a mutant female to female mutants, type 0 male mutants and type 1 male mutants in the next generation, respectively. The first element is equal to 1, since a female produces on average one (surviving) female offspring. In addition, the female also produces on average one male offspring. With probability $1-t$ this male will be of type 0 (no ornamentation) and survive to adulthood. With probability t, the male will be of type 1 and survive with probability $1-s$ to adulthood. The other two columns correspond to the contributions of type 0 and type 1 mutant males to the various types of mutants in the next generation. These columns correspond to column 1 multiplied by the per capita number of matings (Q_0^* and Q_1^*) of the two types of male. The factor $\frac{1}{2}$ in (A12) reflects the fact that each individual has one father and one mother and prevents double counting of offspring. Notice that the matrix elements do not depend on p, and that the dependence on p^* and t^* is indirect (via Q_0^* and Q_1^*).

Invasion fitness. The dominant eigenvalue $W\left(p,t \middle| p^*,t^*\right)$ of the stage transition matrix $\mathbf{A}$ corresponds to the 'invasion fitness' of the rare mutant. For the resident population, the dominant eigenvalue is equal to one (reflecting the fact that this population is stationary). If $W > 1$, the mutant will increase in relative frequency, while it will go extinct if $W < 1$.

To determine the properties of the invasion fitness function, we first have to investigate the stage transition matrix $\mathbf{A}_{res} = \mathbf{A}\left(p^*, t^* \,\middle|\, p^*, t^*\right)$ of the resident population. The right eigenvector of the dominant eigenvalue 1 gives the stable distribution of the three types of individuals in the resident population (which via (A11) affect Q_0^* and Q_1^*):

$$u_f^* : u_{m0}^* : u_{m1}^* = 1 : (1-t^*) : (1-s)t^*. \tag{A13}$$

The left eigenvector of $\mathbf{A}_{res}$ corresponds to the reproductive values of the three types:

$$v_f^* : v_{m0}^* : v_{m1}^* = 1 : Q_0^* : Q_1^*. \tag{A14}$$

Using a standard result of life history theory (Taylor 1996), the dependence of $W\left(p, t \,\middle|\, p^*, t^*\right)$ on *p* and *t* can now be determined without actually calculating invasion fitness (which can be quite tedious). In fact, the partial derivatives of *W* at (p^*, t^*) are of the form:

$$\frac{\partial W(t, p \mid t^*, p^*)}{\partial t} = \mathbf{v}^{*\mathrm{T}} \frac{\partial \mathbf{A}}{\partial t} \mathbf{u}^* / \mathbf{v}^{*\mathrm{T}} \mathbf{u}^*. \tag{A15}$$

Inserting (A13), (A14) and the partial derivatives of (A12) into this equation yields:

$$\left.\frac{\partial W}{\partial t}\right|_{t=t^*} = (1-s)Q_1^* - Q_0^*, \quad \left.\frac{\partial W}{\partial p}\right|_{p=p^*} = 0. \tag{A16}$$

The total selection differentials are then given by:

$$\begin{aligned} \left.\frac{dW}{dt}\right|_{t=t^*} &= \left(\frac{\partial W}{\partial t} + b_{tp}\frac{\partial W}{\partial p}\right)_{t=t^*} = (1-s)Q_1^* - Q_0^* \\ \left.\frac{dW}{dp}\right|_{p=p^*} &= \left(\frac{\partial W}{\partial p} + b_{pt}\frac{\partial W}{\partial t}\right)_{t=t^*} = b_{pt}\left((1-s)Q_1^* - Q_0^*\right) \end{aligned} \tag{A17}$$

where b_{yx} is the statistical regression coefficient of *y* on *x* (Taylor & Frank 1996), which is assumed to be a positive parameter.

Evolutionarily singular strategies. At an internal ‘equilibrium’ both selection differentials in

(A17) have to be zero, leading to the condition $(1-s)Q_1^* = Q_0^*$, which can be simplified to $t^* = \alpha(p^*)$. Once again, this condition describes a whole set of equilibria. For many preferences, this set is again a straight line. Assume, for example, that females have ‘fixed relative preferences’ as in Kirkpatrick’s model with probability p^* while they mate at random with probability $1-p^*$. Then $\alpha(p^*)$ is given by

$$\alpha(p^*) = p^* \frac{au_{m1}^*}{u_{m0}^* + au_{m1}^*} + (1-p^*)\frac{u_{m1}^*}{u_{m0}^* + u_{m1}^*}. \tag{A18}$$

Equating this expression with t^* yields the same line of equilibria as in Kirkpatrick’s model (see Figure 2*c* in the main text). The approach to equilibrium (via a sequence of gene substitution events), which is also indicated in Figure 2*c*, can be derived from the canonical equation of adaptive dynamics theory (Geritz et al 1998).

Individual-Based Simulation Models of the Fisher Process

Individual-based models of sexual selection are the most recent addition to the set of tools to analyze evolutionary models (Grimm & Railsback 2005); a growing number of sexual selection models makes use of this versatile technique (e.g., Lorch et al 2003, Gavrilets et al. 2007, Kokko et al 2007, Fawcett et al 2007). Here, we discuss an individual-based model on Fisherian sexual selection that is used by Fawcett et al (2007). The source code of this simulation can be found at http://www.rug.nl/biol/theobio/fisher.cpp. A flow diagram of the model is given in Supplemental Figure 2.

Initialization. An individual-based simulation starts with a definition of the individuals initially present and their properties. For sake of comparison to the previous analytical models, we assume that individuals are genetically characterized by their alleles at two haploid loci, one coding for a male ornament *t* and the other coding for a female preference *p*. However, we emphasize that individual-based simulations easily allow for the implementation of complex genetic architectures and genotype-phenotype maps (e.g., Ten Tusscher & Hogeweg 2009). The population is initialized by generating a large collection of males and females (say, n=2000 males and n=2000 females) and randomly assigning ornament and preference alleles to each individual according to some prespecified distribution (e.g. a bivariate normal distribution) (see Supplemental Figure 2, step 1).

Viability selection. Subsequently, the population of males enter a procedure that determines their survival (see Supplemental Figure 2, step 2), whereas all females survive. The simulation assumes that a male's survival probability v is given by a Gaussian function $v(t) = \exp(-ct^2)$, where the parameter c determines the strength of viability selection. However, in contrast to the aforementioned deterministic models, survival is implemented in a stochastic fashion (i.e., by letting a chance process decide whether a given male will die or survive). In Supplemental Figure 2 (step 2) males with larger ornaments are more likely to die, but individual males may, by chance, escape mortality.

Mating stage. The surviving males and all females then enter another procedure, in which females choose mates. As in the deterministic models, female mate choice can be implemented in various ways. For example, fixed relative preferences can be implemented by sequentially assigning randomly drawn males to each female, until one of these males is accepted by the female for mating. The probability of accepting any given male depends on both, the female’s preference and the male’s ornament. Alternatively, each female is confronted with a random sample of N males and subsequently mates with the male most closely fitting to her preference (‘best-of-N’ model). A third alternative (implemented by Fawcett et al. 2007) combines the two approaches above: each female samples N males and subsequently mates with male i with a probability that is proportional to i's attractiveness value to the female. Supplemental Figure S2 step 3 shows that large ornamented males are on average more often chosen by females with high values of the preference, but stochastic variation in mate sampling and mate choice reduces the strength of assortative mating to a certain extent.

Reproduction and mutation. After having chosen a mate females reproduce, having their offspring sired by their mate of choice. In the simulation model considered here, all females contribute effectively two offspring to the next generation, at a 1:1 sex ratio (see Supplemental Figure 2, step 4). As a consequence, the population size remains constant over the generations. Upon reproduction, mutation takes place (see Supplemental Figure 2, step 5). The current model assumes a continuum-of-alleles model of mutation, in which preference and ornament alleles present in an individual mutate with probabilities μ_p and μ_t respectively. When mutation takes place, a deviate from a normal distribution with mean 0 and standard deviation σ_μ is added to the current allelic value. The life cycle then repeats itself and males of the next generation enter the juvenile survival stage.

Evolutionary dynamics. Figure 2*d* in the main text illustrates the course of evolution of an individual-based simulation. For similar parameter values as in Lande's model (Figure 2*b*), the system converges to Lande's line of equilibria and subsequently 'drifts' along this line. The irregularities in the evolutionary trajectory clearly illustrate the stochastic nature of an individual-based simulation.

References

Albert AYK, Otto SP. 2005. Sexual selection can resolve sex-linked sexual antagonism. *Science*. 310:119–121.

Arnold SJ. 1985. Quantitative genetic models of sexual selection. *Experientia*. 41:1296-1310.

Bulmer M. 1989. Structural instability of models of sexual selection. *Theor Popul Biol*. 35:195–206.

Fawcett TW, Kuijper B, Pen I, Weissing FJ. 2007. Should attractive males have more sons? *Behav Ecol*. 18:71–80.

Fawcett TW, Kuijper B, Weissing FJ, Pen I. 2011. Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity. *Proc Natl Acad Sci* 108:15925-15930.

Fisher R. 1915. The evolution of sexual preference. *Eugen Rev*. 7:184–192.

Gavrilets S, Vose A, Barluenga M, Salzburger W, Meyer A. 2007. Case studies and mathematical models of ecological speciation. 1. cichlids in a crater lake. *Mol Ecol*. 16:2893–2909.

Geritz S, Kisdi É, Meszéna G, Metz J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol Ecol*. 12:35-57

Grimm V, Railsback SF. 2005. *Individual-based Modeling and Ecology*. Princeton University Press, Princeton.

Iwasa Y, Pomiankowski A. 1994. The evolution of mate preferences for multiple sexual ornaments. *Evolution*. 48:853-867.

Kirkpatrick M. 1982. Sexual selection and the evolution of female choice. *Evolution*. 36:1–12.

Kokko H, Brooks R, McNamara JM, Houston AI. 2002. The sexual selection continuum. *Proc R Soc Lond B Biol Sci*. 269:1331–1340.

Kokko H, Jennions MD, Houde A. 2007. Evolution of frequency-dependent mate choice: keeping up with fashion trends. *Proc R Soc Lond B Biol Sci*. 274:1317–1324.

Lande R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc Natl Acad Sci*. 78:3721–3725.

Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution.* 37:1210-1226.

Lorch PD, Proulx S, Rowe L, Day T. Condition-dependent sexual selection can accelerate adaptation. *Evol Ecol Res.* 5:867-881.

Maynard Smith J. 1985. Sexual selection, Handicaps and true fitness. *J Theor Biol.* 115:1-8.

McNamara JM, Houston AI, Santos MMd, Kokko H, Brooks R. 2003. Quantifying male attractiveness. *Proc R Soc Lond B Biol Sci*. 270:1925–1932.

Pen IR, Weissing FJ. 2000. Sexual selection and the sex ratio: An ESS analysis. *Selection*. 1:111–121.

Pomiankowski A. 1987. The costs of choice in sexual selection. *J Theor Biol*. 128:195–218.

Pomiankowski A, Iwasa Y, Nee S. 1991. The evolution of costly mate preferences I. Fisher and biased mutation. *Evolution*. 45:1422–1430.

Seger J. 1985. Unifying genetic models for the evolution of female choice. *Evolution*. 39:1185–1193.

Seger J, Trivers R. 1986. Asymmetry in the evolution of female mating preferences. *Nature*. 319:771–773.

Takahasi K. 1997. Models of selective mating and the initiation of the fisherian process. *Proc R Soc B* 264:839–844.

Taylor PD. 1996. Inclusive fitness arguments in genetic models of behaviour. *J Math Biol*. 34:654–674.

Taylor PD, Frank SA. 1996. How to make a kin selection model. 1996. *J Theor Biol.* 180:27-37.

Ten Tusscher K, Hogeweg P. 2009. The role of genome and gene regulatory network canalization in the evolution of multi-trait polymorphisms and sympatric speciation. *BMC Evol Biol*. 9:159.

Van Doorn GS, Weissing FJ. 2004. The evolution of female preferences for multiple indicators of quality. *Am Nat*. 164:173-186.

Van Doorn GS, Weissing FJ. 2006. Sexual conflict and the evolution of female preferences for indicators of male quality. *Am Nat*. 168:742-757.

Walsh B, Lynch M. 2012. *Evolution and Selection of Quantitative Traits: I. Foundations*. Book Manuscript, available at: http://nitro.biosci.arizona.edu/zbook/NewVolume_2/ newvol2.html.

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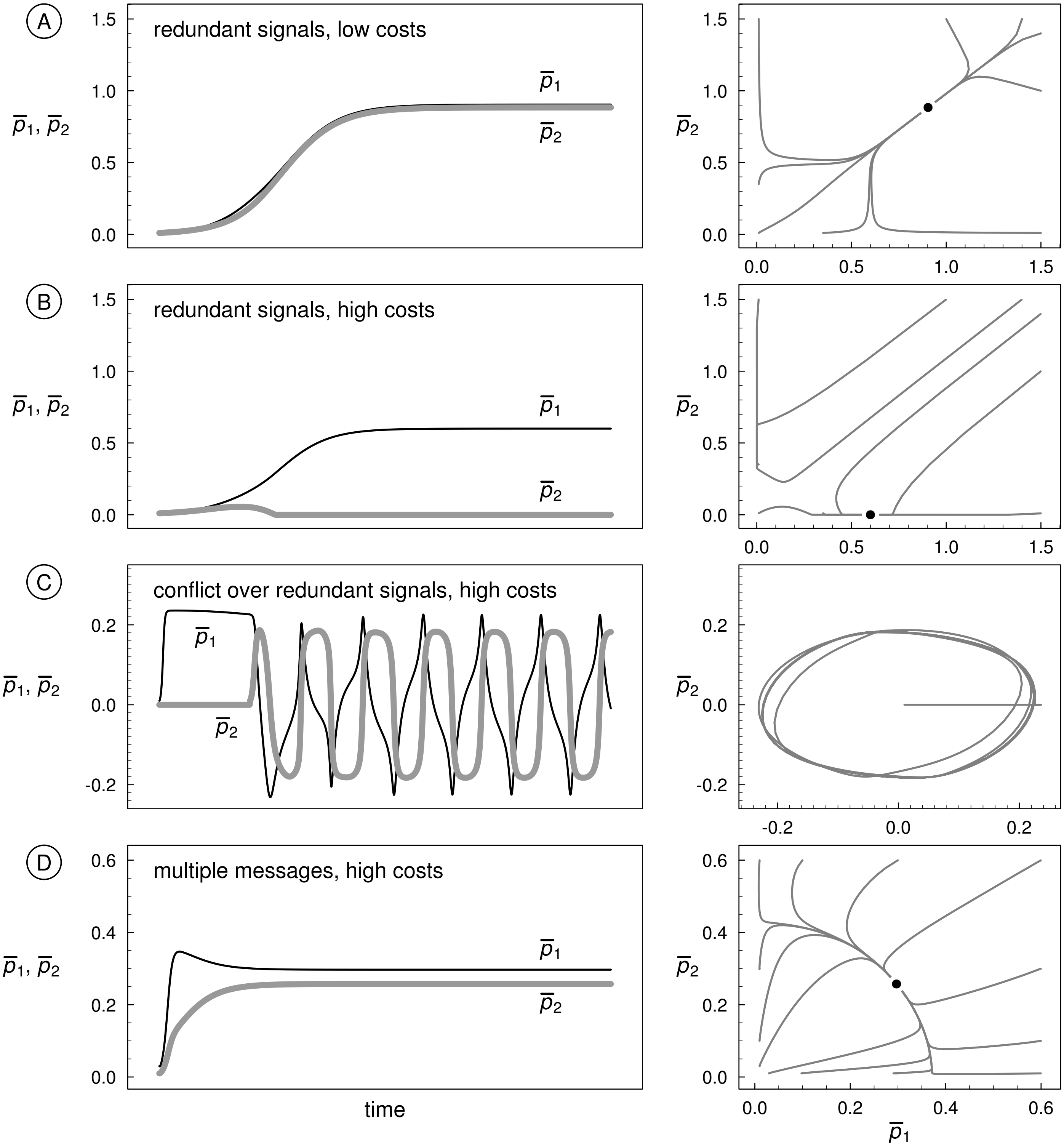
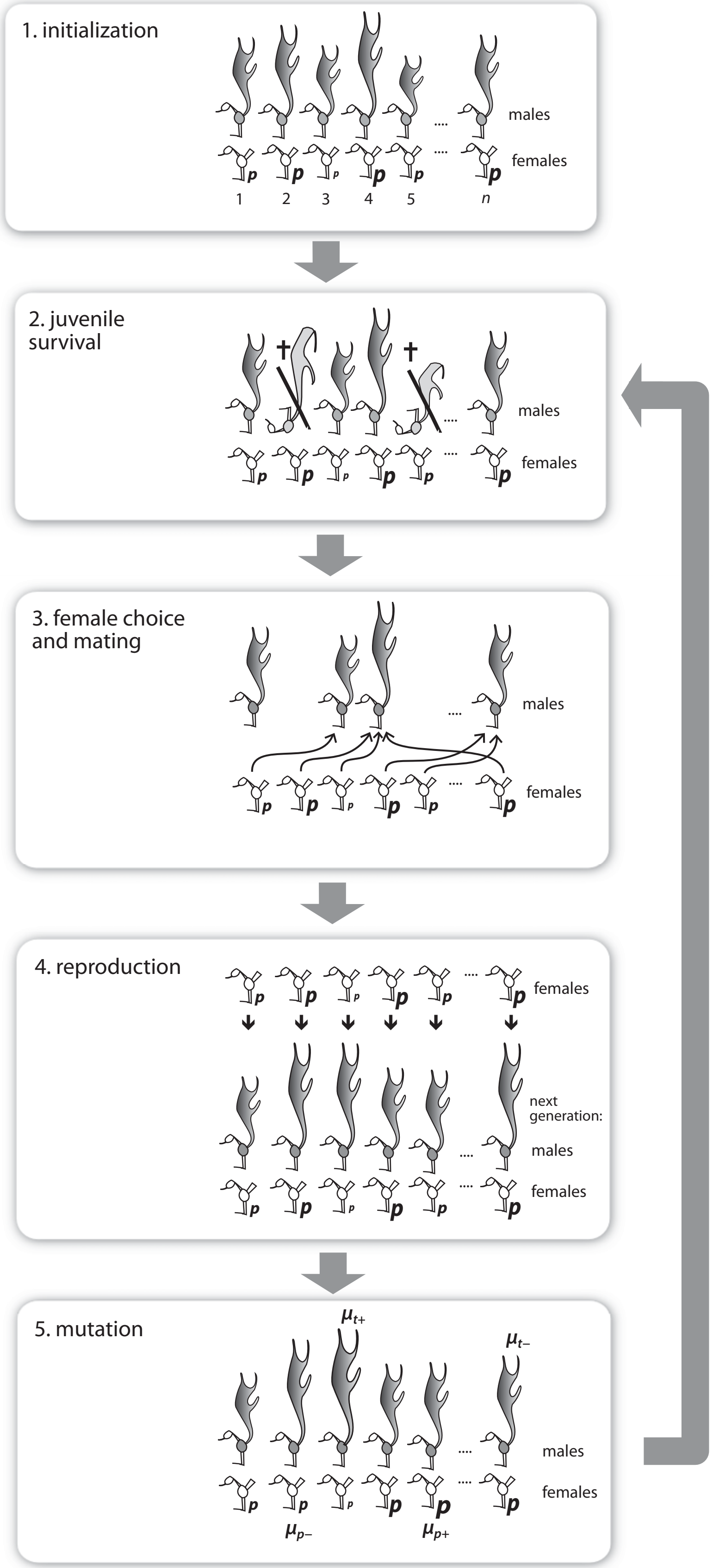
Supplemental Figure 1



Supplemental Figure 1. The evolution of female preferences for multiple indicators of male quality. *Panel A*: multiple female preferences for redundant signals only evolve to stable levels when the cost of expressing multiple preferences is sufficiently low (Iwasa & Pomiankowski 1994). *Panel B*: In contrast, when the cost of expressing multiple preferences is higher, the cost of expressing the first preference ($\overline{p}_1 > 0$) blocks the evolution of any additional preferences ($\overline{p}_2 = 0$), and the evolution of a particular preference towards nonzero equilibrium levels depends on initial conditions. *Panel C*: Nonequilibrium dynamics of preferences and ornaments (for example due to sexual conflict over signaling) can lead to the establishment of multiple preferences for redundant indicators, even when high costs of female preferences would preclude the evolution multiple preferences at equilibrium (van Doorn & Weissing 2006). *Panel D:* multiple female preferences for indicators that each signal distinct components of male quality (“multiple messages”) can evolve to stable levels, even in the face of high costs (van Doorn & Weissing 2004).

Supplemental Figure 2.



Supplemental Figure 2. Flow diagram of an individual-based simulation, reflecting a population of Arnold's bird of paradise (Arnold 1985) that experiences the Fisher process. Step 1: the population is initialized by generating a population of n males (that vary in tail length) and n females (that vary in their preferences for tail length, p). Step 2: male viability selection takes place, in which males with the smaller ornaments are most likely (but not certain) to survive. Step 3: female choices takes place based on ornaments and preferences (see Supplement S4) and the eventual choices are indicated by black arrows. Males with large ornaments are likely (but not certain) to achieve a high mating rate. Step 4: after fertilization by their male of choice, females reproduce and give rise to the next generation of males and females. Step 5: mutation events can take place (indicated by μ) that can either increase or decrease values of ornaments and preferences (indicated by + or -). After mutation, the next cycle of the program starts again at step 2.