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Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection

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SUMMARY

The evolution of multiple female preferences by Fisher's runaway process is investigated. The main factor determining the evolutionary equilibrium is the joint cost of female choice. Multiple preferences evolve when the joint cost of two preferences is little more than the maximum of either cost alone. However, as the joint choice cost increases, one preference tends to dominate. Other preferences persist but are much weaker. The dominant preference is the one which gives the female the greatest Fisherian benefit (more attractive male offspring) relative to the cost of choice. The genetic mechanism controlling preference and the male trait are not crucial in determining equilibrium. Only when the joint cost becomes extreme will all but one preference be lost. Fisher's process readily explains the presence of multiple sexual ornaments.

1. INTRODUCTION

In many species sexual selection has caused the evolution of multiple sexual ornaments. Male sage grouse, for instance, are adorned with black throat and belly feathers, bright yellow eye markers, inflatable air sacs, spiked tail feathers and make whistle-pop noises during their highly stereotyped strut display (Wiley 1973). In contrast, barn swallows are only slightly sexually dimorphic. Males have marginally elongated tail feathers compared with females.

It has been suggested that single and multiple ornaments have different signalling functions. Møller & Pomiankowski (1993*a*) compared feather ornaments in bird species with single and multiple ornaments. They used fluctuating asymmetry as a measure of individual condition to show whether ornaments have condition-dependent expression (Møller & Pomiankowski 1993*b*). Single ornamented species showed consistent negative correlations of asymmetry with ornament size. Males with larger ornaments had lower asymmetry. These ornaments appear to have condition-dependent expression and are likely to act as indicators of good genes. In contrast, the sex traits of multiple ornamented species showed no correlation between asymmetry and ornament size. The absence of condition-dependent expression is consistent with these traits being Fisher traits.

The purpose of this paper is to investigate when multiple or single sexual ornaments evolve through Fisher's runaway process (Fisher 1930). A model for the evolution of single female preferences is developed in which change in the genetic covariance is tracked. This allows equilibrium to be specified in selective terms. The model is then applied to the evolution of multiple sexual preferences. The conditions leading to the evolution of single or multiple ornaments by

Fisher's process are derived. Our conclusion is that Fisher's process can readily give rise to multiple female preferences for several male ornamental traits. In a companion paper (Iwasa & Pomiankowski 1993) we show how the handicap process can lead to the evolution of multiple ornaments, and then consider how these two forces interact.

2. SINGLE ORNAMENT MODEL

The evolution of male ornament size (t) and female mate preference (p) will be studied by using a two-trait model of sexual selection, previously developed by Pomiankowski *et al.* (1991). Ornament size and mate preference are assumed to have an additive, polygenic basis. By using an assumption of weak selection (fitness changes little over the range of phenotypic variation; see §3), the change in the mean trait values per generation satisfies

$$\begin{pmatrix} \Delta \bar{t} \\ \Delta \bar{p} \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_t & B_{tp} \\ B_{tp} & G_p \end{pmatrix} \begin{pmatrix} \beta_t \\ \beta_p \end{pmatrix} + \begin{pmatrix} -u \\ 0 \end{pmatrix}. \quad (1)$$

The $\frac{1}{2}$ indicates the sex-limited expression of t and p . G_t , G_p and B_{tp} are the terms for the additive genetic variances and covariance; β_t and β_p are the selection gradients acting on the ornament and female preference, and are evaluated at the population means $t = \bar{t}$, $p = \bar{p}$,

$$\left. \begin{aligned} \beta_t &= \partial \ln W_m / \partial t, \\ \beta_p &= \partial \ln W_f / \partial p. \end{aligned} \right\} \quad (2)$$

W_m and W_f are the lifetime fitness of males and females, respectively. The standard nature of male and female fitness in models of sexual selection are

$$\left. \begin{aligned} W_m &= e^{-ct^2} e^{a\bar{p}(t-\bar{t})}, \\ W_f &= e^{-bp^r}. \end{aligned} \right\} \quad (3)$$

Male fitness is affected by both natural and sexual selection. The optimal expression of the male trait under natural selection occurs when $t = 0$. Viability declines symmetrically either side of this value. The parameter c determines how quickly male survival falls around the natural selection optimum. Male mating success is determined by the second term in equation (3). Females are assumed to assess males with respect to the mean male trait (\bar{t}). Mating success increases with ornament size at a rate proportional to the average female preference \bar{p} .

The effect of preference is mediated by a . This calibrates the increase in mating success caused by an increase in ornament size; a is a property of both male and female behaviour. From the female's view point it reflects the efficiency of preference in identifying males with larger ornaments. From the male's view point it reflects the effectiveness of male signalling in causing increased mating success. It also reflects various life-history, ecological and physiological properties. For instance, lower values of a will be common in monogamous species because there are fewer male mating opportunities compared with polygamous species; a densely wooded environment will restrict the efficacy of visual or auditory signals compared with a more open habitat; greater female sensory discrimination will allow small differences in male ornamentation to result in significant differences in mating success.

The strength of a female's preference is measured by p . Females with positive p preferentially select mates with larger than average ornaments. Females with $p = 0$ are equally likely to mate with any male, and those with negative p prefer males with smaller than average ornaments. We use the 'psychophysical' model among mathematical expressions for female preference (Lande 1981). The exact model of choice does not affect the evolutionary outcome. This model is followed because of its simplicity.

Like the male trait, preference is subject to natural selection. Females risk predation and expend time and energy discriminating between males. There are also opportunity costs associated with choice. A female moving between the territories of potential mates risks losing males examined earlier, especially when mating removes males from the pool of potential mates, as in monogamous species (Slagsvold *et al.* 1988). Female costs are minimized when there is no discrimination ($p = 0$) and increase symmetrically with the strength of female preference. The cost coefficient b determines how rapidly fitness declines around the optimum. The parameter γ determines the shape of this decline. For instance, if costs are negligible for weak discrimination but increase rapidly once the magnitude of preference becomes large, this suggests that $\gamma \geq 2$. Substituting the expressions for male and female fitness into equation (2) gives

$$\left. \begin{aligned} \beta_t &= a\bar{p} - 2c\bar{t}, \\ \beta_p &= -\gamma b\bar{p}^{\gamma-1}. \end{aligned} \right\} \quad (4)$$

The final term in equation (1) is u , the mutation bias acting on the male character. We have previously

argued that random mutation is likely to reduce rather than increase the size of sexual ornaments (Pomiankowski *et al.* 1991). Although the magnitude of this effect may be small, mutation bias is important as it allows the establishment of costly female preference (Pomiankowski *et al.* 1991). Without mutation bias (or an equivalent force) this is not possible.

3. PARAMETER MAGNITUDE

In deriving the basic equation, we adopt a weak selection assumption (Pomiankowski *et al.* 1991; Iwasa *et al.* 1991): fitness changes slowly over the range of ornament size and strength of preference in the population. This means that the coefficients a (ornament effectiveness), b (cost of choice) and c (the cost of ornament production and maintenance) are small in magnitude.

A further assumption is made to simplify the analysis. We consider that b (female choice cost) and u (mutation bias) are small in comparison with the other parameters, a , c , G_t and G_p . This follows the traditional theoretical view of sexual selection which initially neglected b and u (Lande 1981; Kirkpatrick 1982). It is now known that these parameters are essential in defining the evolutionary equilibria (Pomiankowski 1987; Bulmer 1989; Pomiankowski *et al.* 1991). However, it seems likely that the pressure of mutation will be a lower order of magnitude than the standing genetic variance, $u \ll G_t, G_p$. In addition, the cost of choice is often likely to be considerably smaller than the cost imposed by ornamentation or the efficiency of choice itself, $b \ll a, c$ (see, for example, Gibson & Bachman 1991).

The additive genetic variances, G_t and G_p , are produced by a balance between mutational input and loss through selection. For simplicity we assume that the genetic variances are constant.

To estimate the genetic covariance B_{tp} , we need to model the underlying genetics. Consider a set of unlinked loci that additively control the value of t and a second set controlling p . By definition, females with larger than average p tend to mate with males with larger than average t . A positive correlation of mother's p and father's t produces a positive association of the genetic values of t and p in offspring. However, each generation random recombination tends to break down any existing linkage. Stabilizing selection with respect to t and p also affects the genetic covariance. These forces can be combined to derive the change per generation and equilibrium genetic covariance (details in Appendix 1):

$$B_{tp} \approx (a/2) G_t G_p. \quad (5)$$

This is a surprisingly simple result. It will prove to be of great utility in the next sections. The equilibrium covariance is primarily determined by a , the effectiveness of the male ornament in causing non-random mating. Recombination cancels out in the determination of the equilibrium value because it equally affects the creation and loss of covariance. Under the weak selection assumption, the effect of stabilizing

selection is of a lower order of magnitude and does not significantly affect the equilibrium covariance.

4. FAST AND SLOW DYNAMICS

If we look at the dynamics of the model, trajectories tend to converge quickly to a line of quasi-equilibria and then move slowly along this line, converging on the equilibrium (figure 1). This two-step behaviour is due to the different magnitude of the parameters. We can decompose this behaviour into fast and slow dynamics, a technique that is common in population biology (see, for example, Schaffer 1981). This reduces the dimensionality of the model to a more manageable size that is easier to understand.

In the fast dynamics we neglect the small terms u and b . This gives a good, short-term approximation, over a number of generations less than the inverse of these quantities $1/b$ and $1/u$,

$$\begin{pmatrix} \Delta \bar{t} \\ \Delta \bar{p} \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_t & B_{tp} \\ B_{tp} & G_p \end{pmatrix} \begin{pmatrix} \beta_t \\ 0 \end{pmatrix}. \tag{6}$$

As is well known the fast dynamics leads to a line of quasi-equilibria defined as $\beta_t = 0$ (Lande 1981). On this line, $\bar{t} = \hat{t}(\bar{p}) = a\bar{p}/2c$. We assume that the line of quasi-equilibria is attractive and cannot be unstable (Lande 1981). This means the slope of the evolutionary trajectory B_{tp}/G_t is always less than the slope of the line $2c/a$, which is reasonable under our assumptions about parameter magnitudes.

Once the population approaches closely to the line of quasi-equilibria, we can no longer neglect u or b . Evolutionary movement after convergence is described by the slow dynamics. The population (\bar{t}, \bar{p}) lies in the region of the line at $\bar{t} = \hat{t}(\bar{p}) + \epsilon x(\bar{p})$, where ϵ is a small constant of the same order of magnitude as b

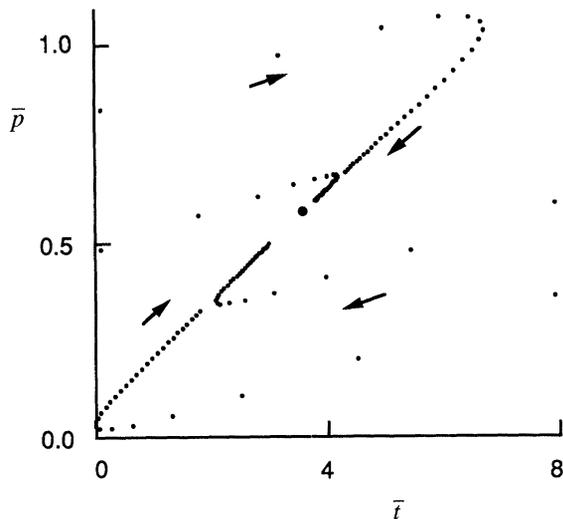


Figure 1. Fast and slow dynamics showing the evolution of the mean female preference (\bar{p}) and mean male ornament size (\bar{t}). Several trajectories are plotted by dots that indicate the location of the population every 100 generations. The population evolves quickly to a line of quasi-equilibria under the fast dynamics and then slowly towards equilibrium under the slow dynamics. Parameters are $a = 0.2$, $b = 0.0004$, $c = 0.015$, $\gamma = 3$, $u = 0.002$, $G_t = G_p = 0.5$, $B_{tp} = 0.025$.

and u . Substituting this definition of \bar{t} into equation (1) allows the evolutionary change to be defined (see Appendix 2):

$$\Delta \bar{p} = (G_p/2) (-\gamma b \bar{p}^{\gamma-1} + ua). \tag{7}$$

The first term in the brackets is β_p , the selection gradient acting on female preference due to the cost of choice. This term is always negative for $\bar{p} > 0$, and hence acts to reduce the average mate preference towards $\bar{p} = 0$. The second term, ua , indicates the indirect genetic benefit arising from mate choice. This is proportional to the mutation bias on the male trait (u) and the efficiency of choice (a). It favours females who spend effort in mate discrimination because they will bear attractive sons with higher mating success. Equilibrium is reached at $\Delta \bar{p} = 0$, which to leading order lies at,

$$\left. \begin{aligned} \bar{p} &= (ua/\gamma b)^{1/(\gamma-1)}, \\ \bar{t} &= (a/2c) (ua/\gamma b)^{1/(\gamma-1)}. \end{aligned} \right\} \tag{8}$$

The leading order value of equilibrium \bar{t} is given by substitution into $\bar{t} = a\bar{p}/2c$. The equilibrium is stable because the cost of trait production increases with size faster than the benefit (note we assume $\gamma > 1$). As previously observed (Pomiankowski *et al.* 1991), mutation bias plays an indispensable role in maintaining a positive evolutionary equilibrium. In the absence of mutation bias, $u = 0$, the equilibrium lies at the natural selection optimum $\bar{p} = 0$, $\bar{t} = 0$. What is far clearer now is the dependence of the equilibrium on the ecological parameters a , b and c . Previously, equilibrium was defined by the genetic parameters G_t , G_p and B_{tp} as well (Pomiankowski *et al.* 1991).

5. MULTIPLE TRAITS

We now consider the evolution of multiple female preferences, each for a different male trait. Although we can easily generalize the result, to make the mathematics less cumbersome, we concentrate on two male traits, t_1 and t_2 , with two corresponding female preferences, p_1 for t_1 , and p_2 for t_2 . Modifying equation (1), the evolutionary dynamics become

$$\begin{pmatrix} \Delta \bar{t}_1 \\ \Delta \bar{p}_1 \\ \Delta \bar{t}_2 \\ \Delta \bar{p}_2 \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_{t_1} & B_{t_1 p_1} & B_{t_1 t_2} & B_{t_1 p_2} \\ B_{t_1 p_1} & G_{p_1} & B_{t_2 p_1} & B_{p_1 p_2} \\ B_{t_1 t_2} & B_{t_2 p_1} & G_{t_2} & B_{t_2 p_2} \\ B_{t_1 p_2} & B_{p_1 p_2} & B_{t_2 p_2} & G_{p_2} \end{pmatrix} \begin{pmatrix} \beta_{t_1} \\ \beta_{p_1} \\ \beta_{t_2} \\ \beta_{p_2} \end{pmatrix} + \begin{pmatrix} -u_1 \\ 0 \\ -u_2 \\ 0 \end{pmatrix}. \tag{9}$$

Combining across the two characters, the selection differentials (evaluated at the population means) are

$$\beta_{t_1} = \frac{\partial}{\partial t_1} \ln W_m = \frac{\partial}{\partial t_1} \left(\sum_{i=1}^2 a_i \bar{p}_i (t_i - \bar{t}_i) - \sum_{i=1}^2 c_i t_i^2 \right), \tag{10a}$$

$$\beta_{p_1} = \frac{\partial}{\partial p_1} \ln W_f = \frac{\partial}{\partial p_1} \left\{ -b \left[\sum_{i=1}^2 (\lambda_i p_i)^{1/\theta} \right]^{\gamma\theta} \right\}, \tag{10b}$$

with similar expression for β_{t_2} and β_{p_2} .

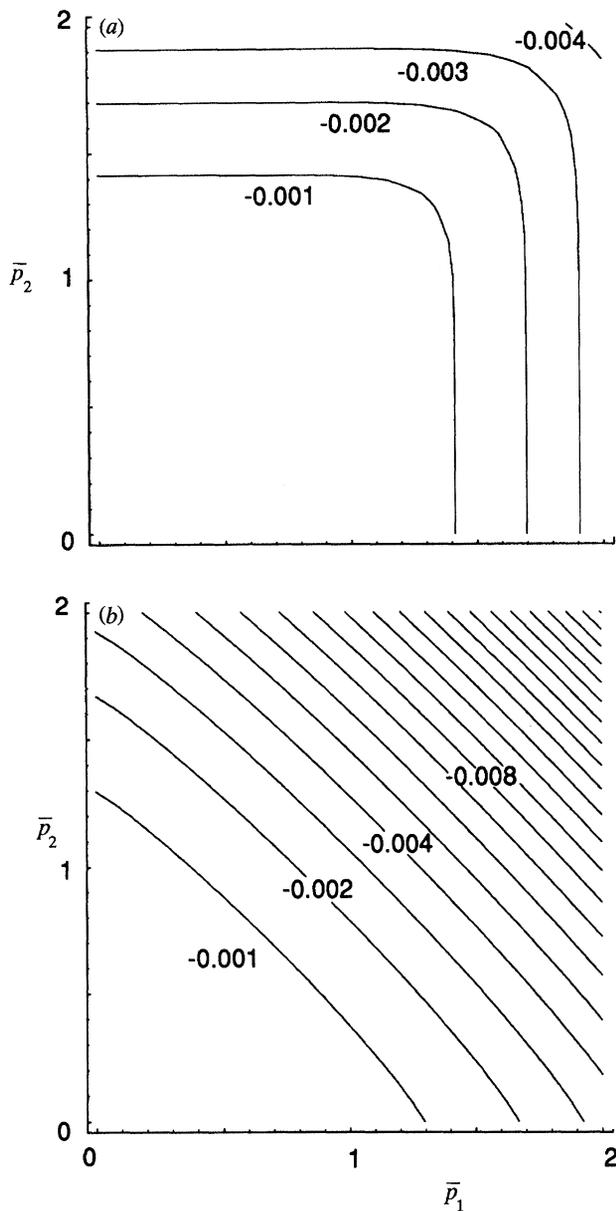


Figure 2. Contour of the cost to females of mate choice using two preferences. (a) $\theta = 0.1$; when θ is small preference for multiple traits does not greatly increase the cost of choice compared to choice using a single trait. (b) $\theta = 0.9$; when θ is large, use of both traits is accompanied by a large cost. Parameters are the same as in figure 1, and $\lambda_1 = \lambda_2 = 1$.

The two ornaments have independent effects on mate choice; female preference for one male character does not extend to the other. We assume that the cost of producing two ornaments simultaneously is simply the sum of the cost of producing each trait independently. This view is adopted because it simplifies the ensuing analysis. It is justified by our observation that interactions in the cost of multiple ornaments are less important than interactions in the cost of female mate preference in determining whether a single or multiple traits evolve.

Female fitness is determined by the combined effect of choice for both male traits. If there is no interaction, the cost of each preference combines multiplicatively and $\theta = \gamma^{-1}$. There are two extreme forms of interaction. First, as $\theta \rightarrow 0$ the overall cost becomes no

more than the maximum cost when either preference is considered alone (figure 2a). Given that females already select males by using one trait ($p_1 > 0$), the initial spread of a second preference p_2 does not greatly increase the overall cost of mate choice. For instance, if females already visit leks and spend time examining male wing plumage, then consideration of male bill colour at the same time may not significantly alter choice costs. At the opposite extreme, as $\theta \rightarrow 1$, costs combined in an supermultiplicative manner (figure 2b). A second preference greatly increases choice costs. For example, females selecting mates by using singing may require quite different sensory capabilities or need to inspect males close by to assess visual displays as well. If females are already time limited, then the additional time required to select males by using a second criterion will significantly increase costs.

Following our previous assumptions about parameter values, a_1, a_2, c_1 and c_2 are small, and u_1, u_2, b_1 and b_2 are very small. Genetic covariances between the male characters and the corresponding female preferences, $B_{t_1 p_1}$ and $B_{t_2 p_2}$, are created automatically by mate choice. Epistatic interactions in the costs of the two preferences creates genetic covariance $B_{p_1 p_2}$ between them. By association, the three other covariances $B_{t_1 p_2}, B_{t_2 p_1}$ and $B_{t_1 t_2}$ will also be non-zero, even though there is no direct cause underlying these covariances.

The analysis proceeds using the same techniques as the single trait model. First, we derive the fast dynamics, which describes the quick convergence of the population to a surface of quasi-equilibria,

$$\bar{t}_1 = \hat{t}_1(\bar{p}_1) = a_1 \bar{p}_1 / 2c_1 \quad \text{and} \quad \bar{t}_2 = \hat{t}_2(\bar{p}_2) = a_2 \bar{p}_2 / 2c_2. \tag{11}$$

After convergence to the surface, further evolution of the population occurs through the slow dynamics. As before we substitute $\bar{t}_1 = \hat{t}_1(\bar{p}_1) + \epsilon x(\bar{p}_1)$ and $\bar{t}_2 = \hat{t}_2(\bar{p}_2) + \epsilon x(\bar{p}_2)$ into equation (9) and rearrange to give (Appendix 3)

$$\begin{aligned} \Delta \bar{p}_1 &= (G_{p_1} / 2) (\beta_{p_1} + u_1 a_1) + (B_{p_1 p_2} / 2) (\beta_{p_2} + u_2 a_2), \\ \Delta \bar{p}_2 &= (G_{p_2} / 2) (\beta_{p_2} + u_2 a_2) + (B_{p_1 p_2} / 2) (\beta_{p_1} + u_1 a_1). \end{aligned} \tag{12}$$

The selection gradient with respect to p_1 is

$$\beta_{p_1} = -\gamma b \lambda_1 \left(\sum_{i=1}^2 (\lambda_i \bar{p}_i)^{1/\theta} \right)^{\gamma\theta-1} (\lambda_1 \bar{p}_1)^{(1-\theta)/\theta}, \tag{13}$$

and that with respect to p_2 has the same form (except the suffix is changed). If we assume that $\gamma > 1$, the system always has a positive equilibrium. This is globally stable because equation (12) is a Lyapunov function (see Appendix 4).

If both mutation biases are positive, then both \bar{p}_1 and \bar{p}_2 must be greater than zero. Hence we can conclude that, at equilibrium, both traits are used simultaneously as male ornaments. The equilibrium is found by setting $\Delta \bar{p}_1 = \Delta \bar{p}_2 = 0$ and substituting for the selection gradients. After some arithmetic, the equilibrium conditions are converted to the following two

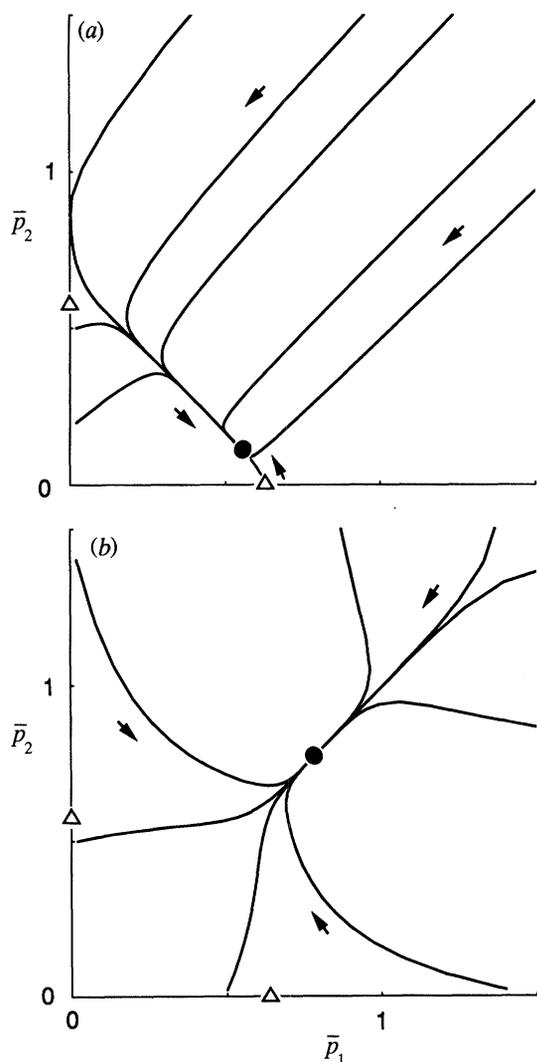


Figure 3. Slow dynamics and equilibria when there are two female preferences (p_1 and p_2) for two Fisher traits. Stable equilibria are shown as filled circles, which are globally stable. Triangles on both axes are equilibria when only one female preference is considered, but are not equilibria when both preferences can evolve. Two conditions are shown; (a) $\theta = 0.9$, and (b) $\theta = 0.1$. Other parameters are $a_1 = 0.24$, $a_2 = 0.2$, $b = 0.0004$, $\gamma = 3$, $\lambda_1 = \lambda_2 = 1$, $u_1 = u_2 = 0.001$, $G_i = G_p = 0.5$, $B_{p_1 p_2} = 0$.

conditions. First we define the relative exaggeration of the two preferences,

$$\frac{\bar{p}_1}{\bar{p}_2} = \frac{\lambda_2 (u_1 a_1 / \lambda_1)^{\theta/(1-\theta)}}{\lambda_1 (u_2 a_2 / \lambda_2)^{\theta/(1-\theta)}}. \quad (14a)$$

The second condition is an expression of the displacement of the population from the natural selection optimum. This is equal to the decrease of female (logarithmic) fitness from its optimum,

$$b \left(\sum_{i=1}^2 (\lambda_i \bar{p}_i)^{1/\theta} \right)^{\gamma\theta} = b \left(\sum_{i=1}^2 \left(\frac{u_i a_i}{\gamma b \lambda_i} \right)^{1/(1-\theta)} \right)^{\frac{\gamma(1-\theta)}{\gamma-1}}. \quad (14b)$$

Figure 3 illustrates the equilibrium and trajectories of the model. The location of the equilibrium in general is given in Appendix 4. We concentrate on the two extreme cases for the sake of clarity. When θ is large, the cost to the female of using multiple signals is

very large. Hence females tend to use only one of the two available traits (figure 3a). Specifically in the limit of $\theta \rightarrow 1$,

$$\left. \begin{aligned} \bar{p}_1 &= \frac{1}{\lambda_1} \left(\frac{u_1 a_1}{\gamma b \lambda_1} \right)^{1/(\gamma-1)}, \quad \bar{p}_2 = 0 & \text{if } \frac{u_1 a_1}{\lambda_1} > \frac{u_2 a_2}{\lambda_2}, \\ \bar{p}_1 &= 0, \quad \bar{p}_2 &= \frac{1}{\lambda_2} \left(\frac{u_2 a_2}{\gamma b \lambda_2} \right)^{1/(\gamma-1)} & \text{if } \frac{u_1 a_1}{\lambda_1} < \frac{u_2 a_2}{\lambda_2}. \end{aligned} \right\} \quad (15)$$

The trait exaggerated at equilibrium is the one that gives females the larger fitness advantage, given by the relative benefit to cost ratio ua/λ (u mutation bias, a signal effectiveness, and λ choice cost). At the opposite extreme, the cost to the female of using multiple signals is negligible, and females are predicted to always use both characters (figure 3b). As $\theta \rightarrow 0$,

$$\lambda_1 \bar{p}_1 = \lambda_2 \bar{p}_2 = \left(\sum_{i=1}^2 (u_i a_i / \gamma b \lambda_i) \right)^{1/(\gamma-1)}. \quad (16)$$

7. DISCUSSION

(a) Single preference

It is well established that Fisher's runaway process can cause the evolution of female mating preferences for extreme male traits. Our previous analysis established the conditions for the evolution of costly female preferences (Pomiankowski *et al.* 1991). A necessary condition for costly female preference is that the male ornament is subject to mutation bias ($u > 0$; equation (8)). At equilibrium, biased mutation produces an excess of poorly ornamented males. Females that are choosy are favoured because on average they have more attractive male offspring with higher mating success and higher overall fitness. Without mutation bias ($u = 0$), the only equilibrium occurs when females mate at random ($\bar{p} = 0$). Mutation bias is indispensable for a positive evolutionary equilibrium.

Equilibrium exaggeration of female preference and male ornamentation are now given entirely in terms of selection. Previous quantitative genetic studies have expressed equilibrium as a product of selection and genetic parameters (variances and covariance). Such a form is of limited use because the magnitude of these parameters is unclear (e.g. equation (6) in Pomiankowski *et al.* 1991). However, the genetic covariance between genes for female preference and genes for the male ornament is a product of selection, primarily non-random mating caused by female choice. The per generation change of the genetic covariance can be calculated and its equilibrium value determined (Appendix 1).

The result is very simple. At equilibrium, the covariance is determined by a multiplied by the product of the genetic variance in female preference and male ornamentation (equation (5)). The coefficient a gauges how an increase in ornament size translates into higher mating success. This depends upon the effectiveness of the male signal and the efficiency with which females distinguish changes in

ornament size. These parameters also reflect various life-history, ecological and physiological properties of the species (see §2).

Substituting for the covariance greatly simplifies the equilibrium conditions as all the genetic terms cancel (equation (8)). As already noted, both preference and ornament exaggeration depend on mutation bias (u), which is the ultimate driving force of evolution. They also both increase with the effectiveness of the male signal (a) and decrease with the costs of choice (b and γ). If female choice costs are large then this will severely constrain exaggeration. The cost of male ornamentation (c) has no bearing on the evolution of female preference but does limit exaggeration of the male ornament.

These equations show that exaggeration is possible even if the absolute value of the genetic covariance is small. What matters is the build up of covariance due to non-random mating, not the exact genetic mechanism controlling preference and the male trait. This build up could easily be significant. Positive genetic covariances consistent with Fisher's process have been demonstrated in sticklebacks (Bakker 1993), although doubts exist over the best known measurement in ladybirds (Majerus *et al.* 1986; Ritchie 1992). One restriction on our result is the assumption of an infinite population. If the effective population size is small then genetic drift could disrupt the development of a positive genetic covariance (Nichols & Butlin 1989). However, it is not clear how small populations must be before drift prevents the establishment of genetic covariance through mate choice.

(b) Multiple preferences

The main thrust of this paper has been to understand how Fisher's runaway process gives rise to multiple sexual traits. One obvious evolutionary route is that males exploit a single preference in several ways. For example, Burley (1981) has shown how the attachment of coloured leg bands to male zebra finches can enhance their attractiveness. This is not because females have natural preferences for leg colour. Females usually select mates by using beak and plumage colours. But this preference appears to be transferable to colour on other parts of the body.

We have excluded this possibility by considering multiple female preferences for separate male traits. The general result is that at equilibrium both female preferences are positive as long as each ornament shows mutation bias. The equilibrium mixture of the two preferences depends on θ , the parameter describing the joint cost of female choice.

If θ is large then choice costs combine in a greater than multiplicative fashion (figure 2*b*). This will be the case when the amount of time available for mate choice is limited or where each preference requires a different sensory capability or behaviour by the female. Under this condition females show strong preference for a single male ornament, with only weak preferences for other male traits (figure 3*a*). The single, strong preference is the one giving the largest Fisherian benefit relative to the cost of choice (equation (16)).

This equilibrium is globally attractive and stable; the trait used is not determined by initial conditions or by any of the genetic parameters. The cost of male ornamentation (c) has no bearing on which preference is established. Male ornamentation follows where female preference evolves.

At the opposite extreme, when θ is small, the joint cost of the two preferences is no more than the maximum of either cost alone (figure 2*a*). For example, examining several as opposed to one male trait may make little difference to choice costs in lekking species if lek attendance is the main female expenditure. Under this condition preference for both male traits readily evolves (figure 3*b*). The relative exaggeration of each preference is determined by its choice cost (λ). Both single-preference equilibria are unstable to the introduction of a second preference when θ is small. As θ increases and costs of choice rise, there is a tendency for one preference to become dominant. But unless θ approaches unity there will always be a mixture at equilibrium.

The conclusion we draw from these results is that multiple preferences and ornaments can easily evolve through Fisher's runaway process. These results are consistent with the observation that lekking species typically have multiple ornaments (Møller & Pomiankowski 1993*a*). In these species it is likely that the cost of multiple preferences do not greatly exceed the costs of a single preference (i.e. θ is small). This conclusion is enhanced by the finding that the ornaments of species with multiple sex traits do not show evidence of condition-dependent expression (Møller & Pomiankowski 1993*a*). It seems most probable that these ornaments act primarily as Fisher traits (enhancing male offspring attractiveness) rather than good genes traits (enhancing offspring survival). However, this interpretation awaits the analysis of multiple preferences generated by the handicap process, which we consider in a companion paper (Iwasa & Pomiankowski 1993).

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APPENDIX 1.

The equilibrium genetic covariance given by equation (5) is justified by the following argument (Barton & Turelli 1991). The computation includes two steps. The first calculates various coefficients of selection, including the one describing the degree of association between traits. The second uses these results to define the dynamics.

The contribution to the next generation of a mating between a male of trait t and a female of trait p is,

$$W(t, p) = \frac{e^{ap(t-t)} e^{-ct^2} e^{-bp^2}}{(e^{ap(t-t)} e^{-ct^2})_t (e^{-bp^2})_p}, \quad (\text{A } 1)$$

where $(\)_t$ indicates the population average with respect to t but still a function of p , and $(\)_p$ indicates the population

average with respect to p but still a function of t . After Taylor expansion of $W(t, p)$ around \bar{t} and \bar{p} , and dividing by the average fitness, we have

$$\frac{W(t, p)}{\bar{W}(t, p)} = 1 + (a\bar{p} - 2c\bar{t})(t - \bar{t}) - \gamma b \bar{p}^{\gamma-1}(p - \bar{p}) - c[(t - \bar{t})^2 - G_t] - [\gamma(\gamma - 1)/2] b \bar{p}^{\gamma-2}[(p - \bar{p})^2 - G_p] + a[(t - \bar{t})(p - \bar{p}) - B_{tp}] + (\text{higher order terms}). \quad (\text{A2})$$

The second term in the right-hand side indicates the intensity of directional selection on t due to female mate preference; the third term, the directional selection with respect to p ; the fourth and the fifth terms, stabilizing selection on the two traits, respectively. The sixth term is for the association of the two characters (Barton & Turelli 1991).

The second step of the analysis is to consider the dynamics of the variances and covariances between loci controlling t and p . We need to specify the genetic systems controlling the traits. The computation explained by Barton & Turelli (p. 244) is for a haploid population, but can easily be extended to diploidy (see Lande 1981). Consider traits t and p have a polygenic basis and that genes affect the magnitude of only a single character. Let ζ_i be the breeding value for the i th locus. In the case of a haploid model the characters are defined as

$$t = \sum_{i \in T} \zeta_i \quad \text{and} \quad p = \sum_{i \in P} \zeta_i$$

where T and P indicate the set of suffixes contributing to t and p . Let C_{ij} be the covariances between i and j loci, hence,

$$G_t = \sum_{ij \in T} C_{ij}, \quad G_p = \sum_{ij \in P} C_{ij} \quad \text{and} \quad B_{tp} = \sum_{i \in P, j \in T} C_{ij}.$$

We can now specify the per generation change of the genetic covariance between t and p , ΔB_{tp} . The full equation includes the third and fourth moments in addition to the covariances (second moments). However, we simplify by using an appropriate approximation, for example, the assumption that the breeding values (ζ_1, ζ_2 , etc.) have a multivariate normal distribution (Lande 1981). The final result is

$$\Delta B_{tp} = -\frac{1}{2}B_{tp} + \frac{a}{4}(G_t G_p + B_{tp}^2) - \frac{c}{2}B_{tp} G_t + (\text{terms including } b) \quad (\text{A3})$$

(see equation (54b) with $r_{ij} = \frac{1}{2}$, in Barton & Turelli (1991)). Our model includes additional terms due to stabilizing selection on female mate preference p . However, these can be ignored as we assume that b is relatively small compared with a and c . By using the weak selection assumption, we can Taylor expand equation (A3) for the equilibrium value. The leading term gives $B_{tp} \approx (a/2) G_t G_p$, which is equation (5) in the text. This result holds so long as $a G_t G_p \ll 1$. An alternative approximation is to assume weak selection without the assumption of normality in the breeding values (Barton & Turelli 1987, 1991). It again produces the same equilibrium definition of B_{tp} .

APPENDIX 2.

The slow dynamics describe evolutionary movement after convergence to the line of quasi-equilibria through the fast dynamics. On the line the selection gradient acting on the male trait vanishes, $\beta_t(\hat{t}(\bar{p}), \bar{p}) = 0$. However, the population is not exactly on the line. Let the population mean traits after converging to the region of the line satisfy $\bar{t} = \hat{t}(\bar{p}) + \epsilon x(\bar{p})$, where ϵ is a small positive constant of the same order of

magnitude as b and u . Putting this form into the original dynamics equation (1) gives

$$\begin{pmatrix} \frac{d\hat{t}(\bar{p})}{d\bar{p}} + \epsilon \frac{dx(\bar{p})}{d\bar{p}} \\ 1 \end{pmatrix} \Delta \bar{p} = \frac{1}{2} \mathbf{G} \begin{pmatrix} \frac{\partial \beta_t}{\partial \bar{t}} \epsilon x(\bar{p}) \\ \beta_p(\bar{p}) \end{pmatrix} + \begin{pmatrix} -u \\ 0 \end{pmatrix}. \quad (\text{A4})$$

Multiplying both sides by \mathbf{G}^{-1} , the second element of the resultant vector equation is,

$$\left[(\mathbf{G}^{-1})_{pt} \frac{d\hat{t}(\bar{p})}{d\bar{p}} + (\mathbf{G}^{-1})_{pp} + O(\epsilon) \right] \Delta \bar{p} = \frac{1}{2} \beta_p(\bar{p}) + (\mathbf{G}^{-1})_{pt}(-u). \quad (\text{A5})$$

By using the assumption that a and c are small in magnitude, and the equality equation (5) derived in Appendix 1, the elements of the inverse of the genetic variance-covariance matrix are

$$(\mathbf{G}^{-1})_{pp} = G_t/|\mathbf{G}| = 1/G_p + [\text{smaller terms}], \quad (\text{A6a})$$

$$(\mathbf{G}^{-1})_{pt} = -B_{tp}/|\mathbf{G}| = -B_{tp}/G_t G_p + [\text{smaller terms}] = -\frac{1}{2}a + [\text{smaller terms}]. \quad (\text{A6b})$$

On the assumption that a is small, we can drop the first term in equation (A5) and simplify to derive equation (7),

$$\begin{aligned} (1/G_p) \Delta \bar{p} &= \frac{1}{2}(\beta_p(\bar{p}) + ua) \\ &= \frac{1}{2}(-\gamma b \bar{p}^{\gamma-1} + ua). \end{aligned} \quad (\text{A7})$$

APPENDIX 3.

The derivation of the slow dynamics for multiple traits is very similar to that for the single-trait case. By using the abbreviations $C = B_{t_1 t_2}$, $B_1 = B_{t_1 p_1}$, and $B_2 = B_{t_2 p_2}$, the multiple trait genetic variance-covariance matrix is,

$$\mathbf{G} = \begin{pmatrix} G_{t_1} & B_1 & \frac{B_1 C B_2}{G_{p_1} G_{p_2}} & \frac{B_1 C}{G_{p_1}} \\ B_1 & G_{p_1} & \frac{B_2 C}{G_{p_2}} & C \\ \frac{B_1 C B_2}{G_{p_1} G_{p_2}} & \frac{B_2 C}{G_{p_2}} & G_{t_2} & B_2 \\ \frac{B_1 C}{G_{p_1}} & C & B_2 & G_{p_2} \end{pmatrix}. \quad (\text{A8})$$

Epistatic interaction between the two female preferences produces a genetic covariance between them, denoted by C . There is no epistatic interaction between the two male traits. Covariance between t_1 and t_2 only arises indirectly through correlations between p_1 and p_2 . We can derive the $B_{t_1 t_2}$ term as follows. Let ρ_{ij} be the genetic correlation between traits i and j ($i, j = t_1, t_2, p_1, p_2$). Then the indirect genetic correlation between t_1 and t_2 is

$$\rho_{t_1 t_2} = \rho_{t_1 p_1} \rho_{p_1 p_2} \rho_{t_2 p_2},$$

which can be rewritten as

$$\frac{B_{t_1 t_2}}{\sqrt{(G_{t_1} G_{t_2})}} = \frac{B_{t_1 p_1}}{\sqrt{(G_{t_1} G_{p_1})}} \frac{B_{p_1 p_2}}{\sqrt{(G_{p_1} G_{p_2})}} \frac{B_{t_2 p_2}}{\sqrt{(G_{t_2} G_{p_2})}}.$$

The other covariances, $B_{t_1 p_2}$ and $B_{t_2 p_1}$, can be derived in a similar way. The elements of the inverse of \mathbf{G} are,

$$\left. \begin{aligned} (\mathbf{G}^{-1})_{p_1 t_1} &= \frac{G_{t_2} G_{p_2} - B_2^2}{|\mathbf{G}|} (-B_1) \left(1 - \frac{C^2}{G_{p_1} G_{p_2}} \right), \\ (\mathbf{G}^{-1})_{p_1 p_1} &= \frac{G_{t_2} G_{p_2} - B_2^2}{|\mathbf{G}|} G_{t_1} \left(1 - \frac{B_1^2 C^2}{G_{t_1} G_{p_1} G_{p_1} G_{p_2}} \right), \\ (\mathbf{G}^{-1})_{p_1 t_2} &= 0, \\ (\mathbf{G}^{-1})_{p_1 p_2} &= \frac{G_{t_2} G_{p_2} - B_2^2}{|\mathbf{G}|} \frac{(-C) G_{t_1}}{G_{p_2}} \left(1 - \frac{B_1^2}{G_{t_1} G_{p_1}} \right). \end{aligned} \right\} \quad (\text{A9})$$

The slow dynamics can be calculated by putting $\bar{t}_1 = \hat{t}_1(\bar{p}_1) + \epsilon x_1(\bar{p}_1, \bar{p}_2)$ and $\bar{t}_2 = \hat{t}_2(\bar{p}_2) + \epsilon x_2(\bar{p}_1, \bar{p}_2)$ into equation (9), where $\hat{t}_1(\bar{p}_1)$ and $\hat{t}_2(\bar{p}_2)$ are the equilibria of the fast dynamics. Then multiplying by \mathbf{G}^{-1} , the p_1 element is

$$\left[(\mathbf{G}^{-1})_{p_1 t_1} \frac{d\hat{t}_1(\bar{p}_1)}{d\bar{p}_1} + (\mathbf{G}^{-1})_{p_1 p_1} + O(\epsilon) \right] \Delta \bar{p}_1 + (\mathbf{G}^{-1})_{p_1 p_2} \Delta \bar{p}_2 + O(\epsilon) = \frac{1}{2} \beta_{p_1}(\bar{p}_1) + (\mathbf{G}^{-1})_{p_1 t_1} (-u_1). \quad (\text{A } 10)$$

Reducing to the leading terms on both sides of equation (A 10) gives,

$$(1/G_{p_1}) \Delta \bar{p}_1 - (C/G_{p_1} G_{p_2}) \Delta \bar{p}_2 = (1/2) \beta_{p_1} + (B_1/G_{t_1} G_{p_1}) u_1.$$

We also have a similar equation for the p_2 element. Combining them we have,

$$\begin{pmatrix} \frac{1}{G_{p_1}} & -\frac{C}{G_{p_1} G_{p_2}} \\ \frac{C}{G_{p_1} G_{p_2}} & \frac{1}{G_{p_2}} \end{pmatrix} \begin{pmatrix} \Delta \bar{p}_1 \\ \Delta \bar{p}_2 \end{pmatrix} = \frac{1}{2} \begin{pmatrix} \beta_{p_1} + u_1 a_1 \\ \beta_{p_2} + u_2 a_2 \end{pmatrix}. \quad (\text{A } 11)$$

Multiplying by the inverse of the matrix on the left-hand side, and taking leading terms,

$$\begin{pmatrix} \Delta \bar{p}_1 \\ \Delta \bar{p}_2 \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_{p_1} & C \\ C & G_{p_2} \end{pmatrix} \begin{pmatrix} \beta_{p_1} + u_1 a_1 \\ \beta_{p_2} + u_2 a_2 \end{pmatrix}, \quad (\text{A } 12)$$

which is the same as equation (12) in the text.

APPENDIX 4.

Female fitness is important in determining change through the slow dynamics. When there are two preferences for two male traits, female fitness (W_f) depends on both p_1 and p_2 . The selection gradient is calculated as the partial derivative of female fitness evaluated as a function of the mean traits,

$$\beta_{p_i} = \frac{\partial}{\partial p_i} \ln W_f(p_1, p_2)_{p_i = \bar{p}_i} = \frac{\partial}{\partial \bar{p}_i} \ln W_f(\bar{p}_1, \bar{p}_2). \quad (\text{A } 13)$$

The change in female preferences per generation is also a function of the mutation biases acting on each of the preferred male traits. We can define a function of \bar{p}_1 and \bar{p}_2 that reflects both these causes of change,

$$V(\bar{p}_1, \bar{p}_2) = \ln W_f(\bar{p}_1, \bar{p}_2) + u_1 a_1 \bar{p}_1 + u_2 a_2 \bar{p}_2. \quad (\text{A } 14)$$

The per generation change of this quantity is,

$$\begin{aligned} \Delta V &= \frac{\partial V}{\partial \bar{p}_1} \Delta \bar{p}_1 + \frac{\partial V}{\partial \bar{p}_2} \Delta \bar{p}_2 \\ &= \frac{1}{2} \left(\frac{\partial V}{\partial \bar{p}_1} \frac{\partial V}{\partial \bar{p}_2} \right) \mathbf{G} \left(\frac{\partial V}{\partial \bar{p}_1} \right) \geq 0. \end{aligned} \quad (\text{A } 15)$$

$\Delta V(\bar{p}_1, \bar{p}_2)$ equals zero when the function $V(\bar{p}_1, \bar{p}_2)$ is maximized. V monotonically increases with time until it reaches this maximum. Because the function has a unique maximum it is a Lyapunov function, and the slow dynamics equation (12) leads to a globally stable equilibrium.

The location of the equilibrium is obtained by setting $\Delta \bar{p}_1 = \Delta \bar{p}_2 = 0$ in equation (12) and substituting for the selection gradient defined in equation (13). We have

$$\gamma b \left(\sum_{i=1}^2 (\lambda_i \bar{p}_i)^{1/\theta} \right)^{\gamma\theta-1} \lambda_1 (\lambda_1 \bar{p}_1)^{(1-\theta)/\theta} = u_1 a_1, \quad (\text{A } 16a)$$

$$\gamma b \left(\sum_{i=1}^2 (\lambda_i \bar{p}_i)^{1/\theta} \right)^{\gamma\theta-1} \lambda_2 (\lambda_2 \bar{p}_2)^{(1-\theta)/\theta} = u_2 a_2. \quad (\text{A } 16b)$$

Dividing equation (A 16a) by equation (A 16b) gives the

ratio of the preferences, equation (14a) in the text. Dividing equation (A 16a) and equation (A 16b) by λ_i , raising to the power of $1/(1-\theta)$, summing these equations and rearranging, gives,

$$\left(\sum_{i=1}^2 (\lambda_i \bar{p}_i)^{1/\theta} \right)^{\frac{\gamma\theta-1}{1-\theta}} = \sum_{i=1}^2 \left(\frac{u_i a_i}{\gamma b \lambda_i} \right)^{1/(1-\theta)}, \quad (\text{A } 17)$$

which is rewritten as equation (14b) in the text. Equation (14a) can be transformed into the following form:

$$\frac{\lambda_1 \bar{p}_1}{(u_1 a_1 / \lambda_1)^{\theta/(1-\theta)}} = \frac{\lambda_2 \bar{p}_2}{(u_2 a_2 / \lambda_2)^{\theta/(1-\theta)}} = X. \quad (\text{A } 18)$$

By replacing p_i in equation (A 17) by equation (A 18),

$$\left(\sum_{i=1}^2 \left(\frac{u_i a_i}{\lambda_i} \right)^{1/(1-\theta)} X^{1/\theta} \right)^{\frac{\gamma\theta-1}{1-\theta}} = \sum_{i=1}^2 \left(\frac{u_i a_i}{\gamma b \lambda_i} \right)^{1/(1-\theta)},$$

which can be rewritten as

$$X = \left\{ \frac{1}{\gamma b} \left[\sum_{i=1}^2 \left(\frac{u_i a_i}{\lambda_i} \right)^{1/(1-\theta)} \right]^{1-\gamma\theta} \right\}^{1/(\gamma-1)}.$$

Then we can use equation (A 18) to give the equilibrium value of mean female preference,

$$\bar{p}_1 = \frac{1}{\lambda_1} \left(\frac{u_1 a_1}{\lambda_1} \right)^{\theta/(1-\theta)} \left\{ \frac{1}{\gamma b} \left[\sum_{i=1}^2 \left(\frac{u_i a_i}{\lambda_i} \right)^{1/(1-\theta)} \right]^{1-\gamma\theta} \right\}^{1/(\gamma-1)}. \quad (\text{A } 19)$$

A similar expression for \bar{p}_2 is given by substituting the suffix 1 with 2.

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