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**DOI**

[10.1046/j.1420-9101.1991.4040637.x](https://doi.org/10.1046/j.1420-9101.1991.4040637.x)

**Publication date**

1991

**Published in**

Journal of Evolutionary Biology

[Link to publication](#)

**Citation for published version (APA):**

Jong, M. C. M., & Sabelis, M. W. (1991). Limits to runaway sexual selection: the wallflower paradox. *Journal of Evolutionary Biology*, 4, 637-655. <https://doi.org/10.1046/j.1420-9101.1991.4040637.x>

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## Limits to runaway sexual selection: The wallflower paradox

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**Key words:** Mate recognition; sexual selection; reproductive isolation; speciation; sex pheromones.

### Abstract

In his mathematical treatment of Fisher's ideas on sexual selection (so-called runaway selection) Lande (1981) predicted that males may evolve increasingly elaborate sexual characters despite opposing viability selection as a consequence of the associated costs.

Lande thereby assumed that female mate preferences are not subject to selection since (1) females are all inseminated and (2) the quantity and quality of their offspring are independent of the female's mate preferences. Kirkpatrick (1985) removed the latter assumption and investigated the consequences for the mean phenotype with respect to both female and male traits. He also explored the dynamics of the (co)-variance matrix by numerical methods.

In this paper we consider a simpler model with just two multi-allelic loci. This enables us to derive explicit expressions for (co)-variances under steady state conditions. Rather than assume natural selection through differential fertility (as in Kirkpatrick, 1985), we take sexual selection on females into account by modelling the preference-dependent risk that females remain unmated.

We argue that this wallflower effect is a realistic feature of any mating system, since it merely depends on the existence of (1) variation in mating preferences and (2) a finite mating season. Our approach provided an insight into the dynamic behaviour of the means of the phenotypes. This is because the dynamics of the means depend on the steady state (co)-variance matrix. Thus, an insight into the former requires explicit expressions for the latter.

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Whereas Lande and Kirkpatrick predicted runaway processes *despite* opposing viability selection, our model predicts a globally stable steady state, i.e. no runaway, even *without* opposing viability selection (under the assumption of an asymptotically stable steady state of the (co)-variances. Admittedly, we have no analytic proof of this stability but only support for it, based on simulations.) The absence of the runaway processes in our model is caused by the wallflower effect, since it imposes constraints on the steady state of the (co)-variance matrix.

When mutational input applies to female traits but not to male traits, explicit expressions for the (co)-variances under steady state conditions can be derived, and these show that: (1) both the genetic covariance and the variance of male traits are equal to zero, but (2) the variance of the female trait exceeds zero. Should there be mutational input influencing the male trait, then these results would suggest that the male-to-female ratio of variances is much smaller than unity. This prediction is of tremendous importance for speciation through founding events.

## 1. Introduction

It is now well established that mate recognition (*sensu* Paterson, 1978, 1982) can be part of the attributes involved in reproductive isolation (Baker *et al.*, 1981; Linn, *et al.*, 1983, 1984; Löfstedt, *et al.*, 1986; Löfstedt, 1990). One may ask whether speciation preceded or ensued from evolution in the mate recognition system. Intuitively, there seems no reason to assume that the latter might be possible. Consider two recently separated populations (say, due to a shift in type of food source). Then why should a male from one population not mate with a female of the other? When males spend little time and energy in producing offspring, it does not make sense to refrain from mating even if the offspring has low viability. However, it all depends on the responsiveness of the male to signals of the female, and both signal production and male response are subject to sexual selection in each of the two original, separate populations. In this paper we shall consider how sexual selection, i.e. selection through differential mating success (see Arnold, 1985), influences the mate recognition properties of both males and females in a single large population. Finally, we shall return briefly to the consequences for speciation.

Imagine an ancestral source population with variation in the signal production of females and the responses of males. A male trait implies a specific response to a particular female signal and a less effective response to all other female signals. Clearly, the possibility of a derived population elsewhere to deviate from the source population critically depends on the relative magnitude of variances in male and female traits. There are three situations: the male-to-female ratio of variances is either (1) much larger than, (2) approximately equal to, or (3) much smaller than unity. In the first case, males of the source population stand a higher chance of responding to females of the derived population than in the third case. Thus, speciation by founding events is promoted by male-to-female variance ratios that are much smaller than unity. For this reason we should consider their evolution in the source population more closely.

Existing models of sexual selection (Lande, 1981; Kirkpatrick, 1985) do not allow the calculation of the male-to-female variances ratio owing to the lack of explicit expressions for the steady state values of the variances. We show that such expressions can be derived by simplifying Lande's polygenic model so that there are just two multi-allelic autosomal loci for the male and female trait respectively.

Our model also differs from existing models in the way females are exposed to selection. Lande (1981) ignored selection on females since he assumed that all females are inseminated and produce offspring whose quality and quantity are independent of mating preferences. Kirkpatrick (1985) extended the model by exploring the consequences of differences in fertility related to the response trait of the male. Though fertility differences may be the inherent consequence of the sexual trait itself (e.g. the peacock's tail), this is not necessarily so. For example, there is no reason to postulate that such differences exist in sex pheromone communication systems in moths. In these systems it seems possible to modify signal production and response without altering costs, e.g. the response to the changed ratio of two structural isomers. We stress that there is another fitness consequence of the female trait that is intrinsic to *all* sexual communication systems: females run a preference-related risk of remaining unmated. This aspect is explicitly modelled, instead of the special assumption of male trait-related fitness differences as made by Kirkpatrick (1985).

Below we shall derive an explicit expression for the male-to-female ratio of variances using a two-locus version of Lande's model as a starting-point. We show that under steady state conditions male-to-female variances are much smaller than unity, with obvious consequences for parapatric speciation.

## 2. The model

Consider two loci, one for the response trait and one for the signal production trait. Both loci are present in males as well as in females (i.e. autosomal traits). In one sex (say males) the response trait is expressed while the signal trait remains hidden. The reverse is the case in the alternative sex (females). In this paper we shall refer to male traits, when they are expressed in males, and to female traits, when they are expressed in females. Thus, the male trait and the female trait are genetically coded in males as well as in females. Selection may act directly on the expressed trait (direct selection), but also indirectly on the associated hidden trait (indirect selection). The latter implicitly assumes that the traits co-vary, but even when the loci for these traits are located on separate chromosomes, genetic covariance will build up as a consequence of assortative mating. Hence, indirect selection plays a crucial role in sexual selection models. In Lande's model the female trait is only subject to indirect selection, whereas the male trait is subject to direct selection. Our model allows both types of selection to act on either sex, and in addition assumes:

- (1) a large population with sexual reproduction in discrete generations.

(2) autosomal genes coding for the male trait and autosomal genes coding for the female trait, with expression conditional on the sex of the individual.

(3) traits expressed in real numbers denoted by  $x$  and  $y$  for the male trait and female trait respectively.

(4) trait values in the population ( $\bar{x}$  and  $\bar{y}$ ) to be Gaussian, distributed with a joint distribution given by:

$$k(x, y) = N(x, y | m_x, m_y, V_{b,x}, V_{b,y}, Cov_L) \quad [1]$$

where  $m$  denotes the mean,  $V$  the variance (the suffix  $b$  refers to the fact that this variance is between individuals), and  $Cov_L$  the linkage disequilibrium covariance. The marginal distribution for the female trait will be referred to as  $g(y)$  and that for the male trait as  $f(x)$ .

[*Remark:* Realizations of random variables (say  $x$ ) are denoted by the corresponding letter without underscoring (say  $x$ ). For the Gaussian (Normal) distributions the parameters are given after the vertical bar, throughout this paper in the same order, first the average(s) and then the variance(s), and in the bivariate case followed by the covariance.]

(5) no crossing-over within a trait, implying that there is no additional variance generated in the offspring. Combined with assumption (4) this means that inheritance is one locus, multi-allelic for each trait.

[*Remark:* The assumption of a joint Gaussian distribution (assumption (4)) for two such traits is due to Lande (1976) and further justified by the numerical explorations of Turelli (1984).]

(6) male and female characters on separate chromosomes, thus any linkage disequilibrium ( $Cov_L$ ) is due to assortative mating only.

(7) that an individual's trait values are the averages of the allelic diploid values inherited from its father and from its mother, i.e. the two alleles are co-dominant.

[*Remark:* Note that some authors use the sum of allelic values as the (breeding) value of an individual (e.g. Falconer, 1981) whereas others use the average (e.g. Bulmer, 1985).]

(8) values inherited by an individual (allelic values) which are not necessarily the values of the parents themselves. The allelic values are assumed to be Gaussian-distributed with a mean equal to the parental value and a segregation variance also referred to as the within-individual variance.

[*Remark 1:* Because no extra variance is generated by crossing-over (assumption (5)) the within-individual variance and the between-individual variance can be calculated from the values of the state variables in the previous generation.]

[*Remark 2:* There are many pairs of allelic values which can generate the same trait value in an individual because the individual's value is the average of the two allelic values (assumption (7)). It follows that each such individual value has its own distribution of allelic values; it is only a matter of convenience that it is *assumed* that all these distributions are Gaussian (assumption (8)) and have the same variance. This will be a good approximation when the selection is weak. See also Appendix I]

(9) males which are always willing and able to inseminate females. Thus, the distribution of the  $x$  values of the males available for mating is the marginal distribution  $f(x)$ .

(10) a distribution of available females which has an average distribution within a generation which is always Gaussian.

[*Remark:* An exact expression for the distribution of available females will be derived below]

(11) encounters between the males and available females occurring at random and with the probability of mating, given the encounter between a female with female trait value  $y$  and a male with male trait value  $x$  being proportional to the response function  $R$ :

$$R(x, y) = \exp\left[-\frac{1}{2}(x - y)^2/R_w\right] \quad [2]$$

This formula corresponds to Lande's (1981) absolute preference model. The parameter  $R_w$  is the Response width. It incorporates all variance which is not additive genetic variance and which is independent of the additive genetic variance, e.g. environmental variance in males and females, the width in responses of each individual, etc.

(12) neither male nor female traits are subject to viability selection, i.e. the traits are only subject to sexual selection not to natural selection *semsu stricto*.

The symbols defined above are summarized in Table 1.

The discrete generation assumption enables us to model the following three processes as successive rather than simultaneous events: (A) the formation of mating pairs, (B) the production of gametes, and (C) the formation of zygotes. These are considered in the following sections.

**Table 1.** Description of the symbols used.

Symbol	Name
$\bar{x}$	male trait.
$\bar{y}$	female trait.
$m_x$	average of the male traits.
$m_y$	average of the female traits.
$V_{b,x}$	between-individual variance for the male trait.
$V_{b,y}$	between-individual variance for the female trait.
$V_{w,x}$	within-individual variance for the male trait.
$V_{w,y}$	within-individual variance for the female trait.
$V_{tot}$	$V_{b,x} + \tau V_{b,y} + R_w$
$Cov_L$	covariance between the male trait and the female trait.
$r_L$	the correlation coefficient $r_L$ corresponding to $Cov_L$ .
$Cov^*$	assortative mating covariance between the males' male trait and the females' female trait.
$\tau$	factor expressing the extent of the wallflower paradox (see formation of mating pairs).
$R_w$	response width, i.e. variance of the response distribution $R(x, y)$ .

(a) *Formation of mating pairs*

The bivariate distribution of  $x$  values among males and  $y$  values among females for all matings in one mating season would be:

$$n(x, y) = \frac{f(x) \cdot g(y) \cdot R(x, y)}{\iint f(x) \cdot g(y) \cdot R(x, y) \, dx \, dy}$$

To take into account that females may remain unmated, assume that the mating season is of fixed duration ( $T$ ) and that each female mates only once, whereas males are polygynous. All males are assumed to be sexually active from the beginning until the end of the season whereas all females are sexually active from the beginning until they obtain a mating. Then, the distribution of male traits among males  $f(x)$  will not change with time ( $t$ ) within the season, but the distribution of female traits among females will change during the season:

$$\frac{\delta g(y, t)}{\delta t} = - \int f(x) \cdot g(y, t) \cdot R(x, y) \, dx \quad [3a]$$

with  $g(y, 0) = g(y)$ .

The change in the bivariate distribution of the individuals that have mated before time  $t$  is:

$$\frac{\delta n(x, y, t)}{\delta t} = f(x) \cdot g(y, t) \cdot R(x, y) \quad [3b]$$

with  $n(x, y, 0) = 0$  for all  $x, y$ .

Since the sexual selection model to be developed in the next section is framed in difference equations expressing generation-to-generation changes, it is not feasible to include within-generation dynamics, while maintaining tractability. Hence, we are in need of an expression for  $g(y)$  (called  $\tilde{g}(y)$ ) that has the same effect as the within-generation dynamics. By solving the above coupled partial differential equations [3a] and [3b] the following modified distribution of female types ( $\tilde{g}(y)$ ) is found:

$$\tilde{g}(y) = g(y, 0) \cdot \frac{(1 - \exp[-\int f(x) \cdot R(x, y) \, dx] \cdot T)}{\int f(x) \cdot R(x, y) \, dx}$$

Thus,  $n(x, y)$  extended to include a finite mating season and the effect of some females remaining unmated, now reads:

$$n(x, y, T) = \frac{f(x) \cdot \tilde{g}(y) \cdot R(x, y)}{\iint f(x) \cdot \tilde{g}(y) \cdot R(x, y) \, dx \, dy}$$

There are two limiting cases with respect to  $T$  for the modified distribution of female traits  $\tilde{g}(y)$ . For small  $T$ , only a few females are mated and the distribution of available females does not change. [Mathematically, this is achieved by writing the expression containing  $T$  as a MacLaurin polynomial and ignoring terms of order two and higher]:

$$\tilde{g}(y) = g(y, 0) = g(y)$$

For infinite  $T$ , all females are mated. Thus, there is no direct sexual selection on female traits as is assumed in Lande's (1981) and Kirkpatrick's (1985) models. In this case the distribution becomes:

$$\tilde{g}(y) \simeq N\left(y|m_y, \frac{V_{b,x} + R_w}{V_{b,x} + R_w - V_{b,y}} \cdot V_{b,y}\right)$$

when  $m_x = m_y$ , as is to be expected near the evolutionary equilibrium. Note that in the two limiting cases the Gaussian distribution is a valid approximation. In the intermediate cases such an approximation remains conjectural.

In these intermediate cases, which will apply in reality, the mating season will be neither short nor indefinitely long. This causes the distribution of available females to change during the season, whereby females that are less attractive initially, gradually become more and more attractive because they suffer less and less from competition with attractive females. What really happens is that less attractive females become gradually over-represented in the population of sexually active females since the attractive ones become sexually inactive. The increasing share of less preferred females may in effect lead to an increased variance among female traits. This is counter-intuitive as one would expect the variance among traits to decrease as a result of direct sexual selection. Therefore, we refer to this phenomenon as *the wallflower paradox*. In retrospect, over a mating season, the males may be viewed to experience a female trait distribution  $\tilde{g}(y)$ . To find the variance of  $\tilde{g}(y)$ , we first replace the distribution  $\tilde{g}(y)$  by an equivalent p.d.f.:

$$\frac{\tilde{g}(y)}{\int \tilde{g}(y) dy}$$

This is done without loss of generality because we normalize  $n(x, y, T)$  anyway. The variance of this equivalent p.d.f. can be calculated by numerical integration of the following expression:

$$\frac{\int (y - m_y)^2 \cdot \tilde{g}(y) dy}{\int \tilde{g}(y) dy}$$

assuming that  $m_x = m_y$ , as is expected near the evolutionary equilibrium.

Numerical integrations of this formula for the variance suggest that this complicated formula can be replaced by  $\tau \cdot V_{b,y}$ , where  $\tau$  is a constant expressing the wallflower paradox. If, in addition, we assume that  $m_x = m_y$  and  $\tilde{g}(y)$  is Gaussian, then the messy expression of  $\tilde{g}(y)$  presented earlier is reduced to:

$$\tilde{g}(y) = g^\tau(y) \simeq N(y|m_y, \tau \cdot V_{b,y}) \quad [4]$$

In theory,  $\tau$  may equal 1 under steady state conditions when the variance of  $y$  values among females ( $V_{b,y}$ ) is zero. Clearly, there can be no effect of wallflowers



when there is nothing to choose. However, since a mutational increase of  $V_{b,y}$  is likely to occur there will be an effect labelled the wallflower paradox ( $\tau > 1$ ).

To indicate the post-mating situation *before* the formation of gametes asterisks will be used. Using expression [4] it is straightforward to calculate the marginal distribution of  $x$  values among males:

$$f^*(x) = \int n(x, y, T) dy \simeq N(x|m_x^*, V_{b,x}^*)$$

where

$$m_x^* = m_x + \frac{V_{b,x}}{V_{tot}} \cdot (m_y - m_x)$$

$$V_{b,x}^* = V_{b,x} - \frac{V_{b,x}^2}{V_{tot}}$$

and

$$V_{tot} = V_{b,x} + \tau \cdot V_{b,y} + R_w.$$

Further, the marginal distribution of  $y$  is:

$$g^*(y) = \int n(x, y, T) dx \simeq N(y|m_y^*, V_{b,y}^*)$$

where

$$m_y^* = m_y + \frac{\tau \cdot V_{b,y}}{V_{tot}} \cdot (m_x - m_y)$$

$$V_{b,y}^* = V_{b,y} + \frac{\{(\tau - 1) \cdot (V_{b,x} + R_w) - \tau \cdot V_{b,y}\} \cdot V_{b,y}}{V_{tot}}$$

As the distribution of mating individuals is bivariate Gaussian (due to [4]), description of this distribution is completed by the following expression for the covariance:

$$Cov^* = \frac{\tau V_{b,y} \cdot V_{b,x}}{V_{tot}}$$

What has been achieved so far, is the derivation of expressions for means, variances and the covariance of the phenotypes. To move on to the start of the next generation, phenotypes should be translated into genotypes, as will be done below.

(b) *The production of gametes*

The joint distributions of fathers' and mothers' gametes for both traits in the population are determined by the means, variances and the covariance at the end of the previous generation (for symbols see Table 1):

$$\begin{aligned}\underline{x}_m &= \underline{x}^* + \underline{a}_m \\ \underline{x}_f &= m_x + \{r_L \cdot \sqrt{V_{b,x}/V_{b,y}} \cdot (\underline{y}^* - m_y) + \underline{b}\} + \underline{a}_f \\ \underline{y}_m &= m_y + \{r_L \cdot \sqrt{V_{b,y}/V_{b,x}} \cdot (\underline{x}^* - m_x) + \underline{c}\} + \underline{d}_m \\ \underline{y}_f &= \underline{y}^* + \underline{d}_f\end{aligned}$$

$\underline{a}_m, \underline{a}_f, \underline{b}, \underline{c}, \underline{d}_m, \underline{d}_f$  are all mutually independent and independent of  $\underline{x}^*$  and  $\underline{y}^*$ , and their distributions are:

$$\begin{aligned}\underline{a}_m &\simeq \underline{a}_f \simeq N(x|0, V_{w,x}) \\ \underline{b} &\simeq N(x|0, (1-r_L^2)V_{b,x}) \\ \underline{c} &\simeq N(y|0, (1-r_L^2)V_{b,y}) \\ \underline{d}_m &\simeq \underline{d}_f \simeq N(y|0, V_{w,y})\end{aligned}$$

The distribution of the expressed allelic trait values ( $\underline{x}_m, \underline{y}_f$ ) follows directly from their distribution among the mating individuals, with an added distribution due to segregation variance (assumption (8)). The hidden trait allelic values ( $\underline{x}_f, \underline{y}_m$ ) follow from the correlation with the expressed value (see also Fig. 1) and again by applying assumption (8).

(c) *Formation of zygotes*

These allelic values ( $\underline{x}_m, \underline{x}_f, \underline{y}_m, \underline{y}_f$ ) can then be used to calculate the values of the distribution in the next generation. As the allelic values are linear combinations of Gaussian-distributed variables they are themselves Gaussian-distributed. Hence, and because the next generation's trait values are a linear function of the allelic values, the distribution of these trait values is also Gaussian. The averages, the between-individual variances, and the genetic covariance in the next generation (indicated by ') follow directly from assumption (7):

$$\begin{aligned}m'_x &= E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f] \\ m'_y &= E[\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f] \\ V'_{b,x} &= E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f]^2 - \{E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f]\}^2 \\ V'_{b,y} &= E[\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f]^2 - \{E[\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f]\}^2 \\ Cov'_L &= E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f][\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f] - E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f]E[\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f]\end{aligned}$$

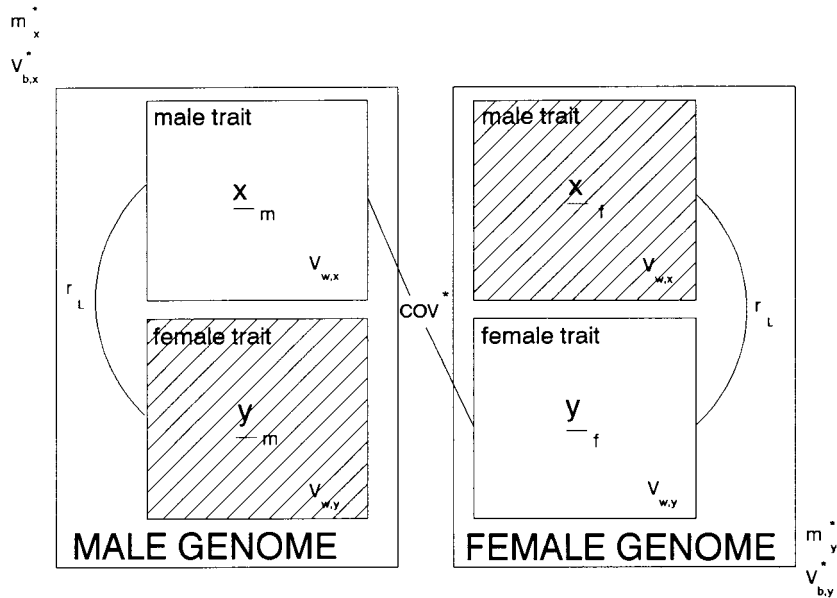


Fig. 1. General structure of the model, showing the relations between the state variables of the population. Hatched squares depict the part of the genome that is hidden. (See text for further explanations).

The total variances between the gametes are:

$$V'_{T,x} = \frac{1}{2}E\underline{x}_m^2 + \frac{1}{2}E\underline{x}_f^2 - \{E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f]\}^2$$

$$V'_{T,y} = \frac{1}{2}E\underline{y}_m^2 + \frac{1}{2}E\underline{y}_f^2 - \{E[\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f]\}^2$$

The within-individual variances can be calculated by subtracting the between-individual variance from the total variance (or, alternatively, by following the procedure as defined in assumption (8) (see Appendix I)):

$$V'_{w,x} = \frac{1}{2}E\underline{x}_m^2 + \frac{1}{2}E\underline{x}_f^2 - E[\frac{1}{2}\underline{x}_m + \frac{1}{2}\underline{x}_f]^2$$

$$V'_{w,y} = \frac{1}{2}E\underline{y}_m^2 + \frac{1}{2}E\underline{y}_f^2 - E[\frac{1}{2}\underline{y}_m + \frac{1}{2}\underline{y}_f]^2$$

This completes the derivation of the difference equations expressing generation-to-generation changes in means, within- and between-individual variances, and the genetic covariance.

### 3. Results and conclusions

There are four processes in the model which change the means, variances and covariance: (1) direct sexual selection (SS), (2) indirect sexual selection, (3) assortative mating, and (4) differential selection on the expressed and hidden copies of the trait.

These processes can be recognized explicitly in the difference equations, expressing generation-to-generation changes in means, variances, and covariance:

$$\Delta m_x = \frac{1}{2} \frac{V_{b,x} - \tau r_L \sqrt{V_{b,x} V_{b,y}}}{V_{tot}} (m_y - m_x)$$

direct    indirect  
SS      SS

[5a]

$$\Delta m_y = \frac{1}{2} \frac{\tau V_{b,y} - r_L \sqrt{V_{b,x} V_{b,y}}}{V_{tot}} (m_x - m_y)$$

direct    indirect  
SS      SS

[5b]

$$\Delta V_{b,x} = \frac{1}{2}(V_{w,x} - V_{b,x}) + \frac{1}{2} \tau r_L \sqrt{V_{b,x} V_{b,y}} \frac{V_{b,x}}{V_{tot}} +$$

random mating    assortative mating

$$\frac{1}{4} \frac{-V_{b,x}^2 + r_L^2 V_{b,x} \{(\tau - 1)(V_{b,x} + R_w) - \tau V_{b,y}\}}{V_{tot}}$$

direct                      indirect  
SS                              SS

[5c]

$$\Delta V_{b,y} = \frac{1}{2}(V_{w,y} - V_{b,y}) + \frac{1}{2} \tau r_L \sqrt{V_{b,x} V_{b,y}} \frac{V_{b,y}}{V_{tot}} +$$

random mating    assortative mating

$$\frac{1}{4} \frac{V_{b,y} \{(\tau - 1)(V_{b,x} + R_w) - \tau V_{b,y}\} - r_L^2 V_{b,x} V_{b,y}}{V_{tot}}$$

direct SS                      indirect SS

[5d]

$$\Delta V_{w,x} = \frac{1}{2}(V_{b,x} - V_{w,x}) - \frac{1}{2} \tau r_L \sqrt{V_{b,x} V_{b,y}} \frac{V_{b,x}}{V_{tot}} +$$

random mating    assortative mating

$$\frac{1}{4} \frac{-V_{b,x}^2 + r_L^2 V_{b,x} \{(\tau - 1)(V_{b,x} + R_w) - \tau V_{b,y}\}}{V_{tot}} +$$

direct                      indirect  
SS                              SS

$$\frac{1}{4} \left\{ \frac{V_{b,x} + \tau r_L \sqrt{V_{b,x} V_{b,y}}}{V_{tot}} (m_y - m_x) \right\}^2$$

differential selection

[5e]

$$\Delta V_{w,y} = \frac{1}{2}(V_{b,y} - V_{w,y}) - \frac{1}{2}\tau r_L \sqrt{V_{b,x} V_{b,y}} \frac{V_{b,y}}{V_{tot}} +$$

random mating    assortative mating

$$\frac{1}{4} \frac{V_{b,y} \{(\tau - 1)(V_{b,x} + R_w) - \tau V_{b,y}\} - r_L^2 V_{b,x} V_{b,y}}{V_{tot}} +$$

direct SS                      indirect SS

$$\frac{1}{4} \left\{ \frac{\tau V_{b,x} + r_L \sqrt{V_{b,x} V_{b,y}}}{V_{tot}} (m_x - m_y) \right\}^2$$

differential selection [5f]

$$\Delta Cov_L = \frac{1}{4} \{ (1 + r_L^2) \frac{\tau V_{b,x} V_{b,y}}{V_{tot}} - 2r_L^2 \sqrt{V_{b,x} V_{b,y}} +$$

assortative mating

$$r_L \sqrt{V_{b,x} V_{b,y}} \left[ \frac{(\tau - 1)(V_{b,x} + R_w) - \tau V_{b,y} - V_{b,x}}{V_{tot}} \right]$$

sexual selection [5g]

Several equilibria exist (see Appendix II), but only one set, i.e. line of equilibria, can be stable:

$$\hat{m}_x = \hat{m}_y, \tag{6a}$$

$$\hat{V}_{b,x} = \hat{V}_{w,x} = 0, \tag{6b}$$

$$\hat{V}_{b,y} = \hat{V}_{w,y} = \frac{(\tau - 1)}{\tau} \cdot R_w, \tag{6c}$$

$$\hat{Cov}_L = 0. \tag{6d}$$

In words, these expressions for the line of equilibria show: (1) matching of complementary traits, (2) absence of between- and within-individual variance of male traits, (3) non-zero variance of female traits depending on (a) the wallflower effect measured by  $\tau (>1)$  and (b) the response width  $R_w$ , (4) absence of genetic covariance, and (5) absence of assortative mating (which causes expression [6d] and  $V_{b,x} = V_{w,x}$ ). When both traits are subject to mutation-selection balance, the expressions [6b] and [6c] translate into the prediction of a low ratio of male-to-female variance.

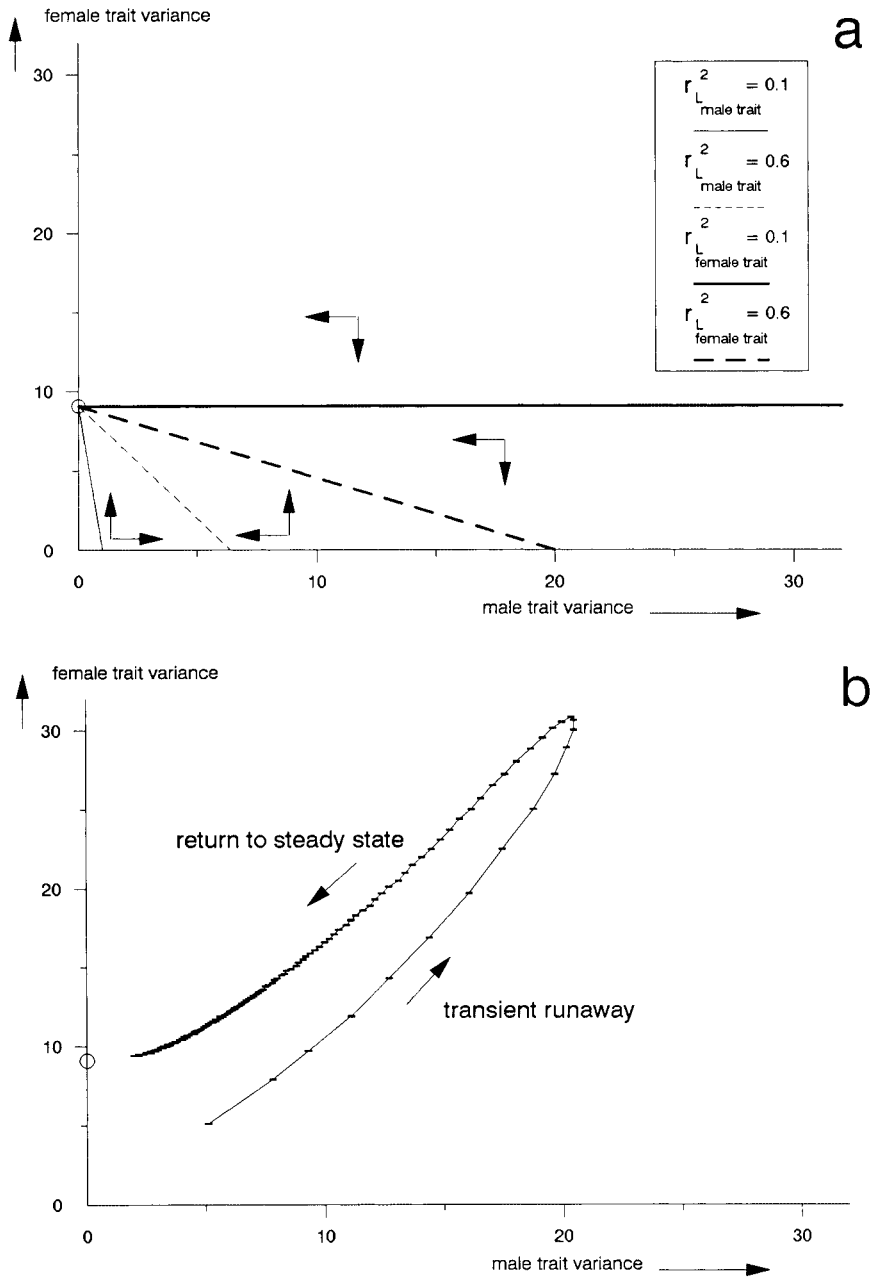
In Appendix IIb the conditions are given for local stability of the line of equilibria. These show that the steady states given under [6] are always locally stable when the probability that some females remain unmated is included (i.e.  $\tau > 1$ ). This is because the wallflower paradox causes the male-to-female variance

ratio ( $V_{b,x}/V_{b,y}$ ) to become less than unity and the genetic covariance to become zero (see Appendix IIb).

How will the system behave away from the line of equilibria [6]? Except for [6] all other possible equilibria are locally unstable. For non-linear systems such as the one under investigation this does not mean that [6] is globally stable. There may be initial conditions that give rise to persistent runaway. Consider the case where  $m_x \neq m_y$ . Here, variances of both traits can increase as a consequence of the differential selection term in the difference equations for within-individual variances ([5e], [5f]). Should the male trait variance exceed that of the female trait, persistent runaway could occur (see Appendix IIb). However, simulations (see Appendix IIc) show that the female trait variance always becomes larger than that of the male trait, causing the runaway process to halt. An example of such a simulation is given in Fig. 2b showing that initially a runaway process may occur but that eventually it returns to a steady state. As an aid in understanding the loop-shape of the simulation trajectory, isoclines (as derived in Appendix IIb) and direction fields for two extreme cases are given in Fig. 2a. In conclusion, the simulations suggest that the steady state expressions given in [6] are globally stable. The runaway type of process is of short duration and depends on special initial conditions away from the steady state.

#### 4. Discussion

The most important conclusion from our work is that for all stable steady states, i.e. on the line of equilibria, the male-to-female variance ratio will be less than unity. This result relies on the inefficiency implicit in any signal-response system; a responder generally does not react with equal efficiency to all possible signals, as evidenced by empirical studies on sex pheromone systems in moths (De Jong, 1987; review by Löfstedt, 1990). This differential efficiency is likely to arise from two sources: (1) response variation between individuals, (2) response variation of a single individual. The work of Cardé *et al.* (1976) suggests that the latter predominates the existing response variation. Hence, while the overall variation is well described by a unimodal response curve, it is reasonable to assume that the individual's response curve is unimodal as well. When this is true and responses vary between individuals, then deviating signals may not be matched by response and vice versa. This shows that females may become wallflowers and thus not only males, but also females are subject to sexual selection, contrary to what has been assumed in the models of Lande (1981) and Kirkpatrick (1985). The existence of wallflowers appears to be essential for the skewed male-to-female variance ratio, but in an unsuspected way. The existence of wallflowers gives rise to an asymmetry in sexual selection: sexual selection on females is less intense than on males. For this asymmetry in sexual selection to be present it is necessary that males increase their fitness by gaining more and more matings, whereas females are constrained with respect to the number of matings (De Jong, *et al.*, in preparation). To be a sufficient condition, however, the mating season should be long enough to allow the



**Fig. 2.** (a) The zero-isoclines for the changes in the total variance of the male trait ( $\Delta V_{T,x} = 0$ ) and of the female trait ( $\Delta V_{T,y} = 0$ ) in the  $V_{b,x} - V_{b,y}$  plane. Two isoclines are shown for both traits:  $r_L = 0.1$  and  $r_L = 0.6$ . (b) A trajectory is drawn to show how between-individual variances can curve away from the equilibrium (indicated by the circle) before returning to it. Initial conditions  $R_w = 100$ ,  $\tau = 1.1$ ,  $m_x \neq m_y$ , and  $r_L = 1.0$ . (Compare to Fig. 3).

population composition of sexually active females to change in the course of the season. These changes comprise an increasing share of females with traits less preferred by males, thereby increasing their probability to mate and contribute to the next generation. The increasing share of less preferred females causes sexual selection on females to be less intense than sexual selection on males, with obvious consequences for the variances. In conclusion, it is not the existence of wallflowers as such, but the increasing share of less preferred females that causes the skewed male-to-female variance ratio. This is what we call the wallflower paradox.

The prediction of a low male-to-female variance ratio implies the absence of runaway selection even without viability selection on the male and female traits (which is likely to halt the runaway process). This is contrary to the results of Lande (1981) and Kirkpatrick (1985). They predicted runaway for some male-to-female variance ratios while ignoring the evolution of the variance ratios themselves. This is not so, as shown here by explicitly modelling the evolution of the (co)-variances. Hence, persistent runaway as conjectured by Fisher (1985) does not take place, but simulations reveal that short bouts of runaway are still possible. We shall term it transient runaway, to stress that after a perturbation averages of the male and female trait may diverge and variances may increase initially, to return eventually to a new steady state (Fig. 2b). This mechanism may occur in addition to random genetic drift along the line of stable equilibria (cf. Lande, 1981).

Turning to the question posed in the introduction we suggest that sexual selection may indeed promote speciation, but in an entirely different way from what has been hitherto proposed (e.g. Rosenzweig, 1978; Pimm, 1979; Seger, 1985). Consider a source population where sexual selection has led to a low male-to-female variance ratio. A sample of this population leading to the establishment of a new population elsewhere may contain deviating females. Evolution through sexual selection in this derived population is likely to lead to a new steady state that differs from the one in the source population. After some period of isolation, therefore, males of the source population are not likely to respond to females of the derived population and *mutatis mutandis* for males of the derived population. Thus, sexual selection in itself may lead to parapatric speciation.

### Acknowledgements

The work presented here benefitted greatly from several discussions with J. A. J. Metz. In addition, comments on earlier drafts of this paper from G. De Jong, P. Stam (who suggested Appendix I), P. M. Brakefield, W. M. Herrebout, C. J. Nagelkerke and R. Roush are gratefully acknowledged.

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Received 8 October 1990;

accepted 8 October 1990.

Corresponding Editor: S. C. Stearns

## Appendix I

An alternative way to derive  $V_{w,x}$  and  $V_{w,y}$  follows directly from assumption (8). Consider the male trait as an example, each individual inherits an allele from its mother ( $x_f$ ) and from its father ( $x_m$ ). The variance between these is:

$$\frac{1}{2}x_m^2 + \frac{1}{2}x_f^2 - \left[\frac{1}{2}(x_m + x_f)\right]^2 = \frac{1}{4}x_m^2 + \frac{1}{4}x_f^2 - \frac{1}{2}x_mx_f$$

The expected value of this is:

$$E\frac{1}{4}x_m^2 + E\frac{1}{4}x_f^2 - E\frac{1}{2}x_mx_f$$

which is equivalent to the expression for  $V'_{w,x}$  given in section 2C in the main text. This equivalence becomes clear by rewriting  $V'_{w,x}$  as follows:

$$\frac{1}{2}E\underline{x}_m^2 + \frac{1}{2}E\underline{x}_f^2 - E(\frac{1}{4}\underline{x}_m^2 + \frac{1}{4}\underline{x}_f^2 + \frac{1}{2}\underline{x}_m\underline{x}_f)$$

**Appendix II***(a) Equilibria*

The equilibria of the difference equations [5] are found by setting their right-hand sides to zero. Whenever  $r_L \neq 1$  the difference equations for the averages ([5a] and [5b]) have only one simultaneous solution:

$$m_x = m_y$$

Thus, for all possible equilibria averages of the traits are equal to each other. It follows from [5c] and [5e] (or equivalently from [5d] and [5f]) that for these difference equations to be zero the difference equations for the total variance of the trait has to be zero. Setting the change in total variance of the male trait to zero (assuming that the averages are equal) yields:

$$V_{b,x} = 0 \quad \text{or} \quad V_{b,x} = \frac{r_L^2(\tau - 1)}{1 - r_L^2(\tau - 1)} R_w - \frac{\tau r_L^2}{1 - r_L^2(\tau - 1)} V_{b,y}$$

Setting the change in total variance of the female trait to zero yields:

$$V_{b,y} = 0 \quad \text{or} \quad V_{b,y} = \frac{\tau - 1}{\tau} V_{b,x} + \frac{\tau - 1}{\tau} R_w - \frac{r_L^2}{\tau} V_{b,x}$$

For  $r_L^2 \neq 1$  there are only two valid combinations, for which  $\Delta V_{T,x}$  and  $\Delta V_{T,y}$  are both zero. For both these solutions the between-individual variance of the male trait is zero and therefore the linkage disequilibrium covariance will be zero and, from [5g], it follows that  $\Delta Cov_L = 0$ .

Since  $V_{b,x} = 0$ , the equation for the covariance between mating partners shows that there is no assortative mating at equilibrium. Therefore, the between-individual and within-individual variances will equal each other. Hence, there are just two sets of equilibria [IIa and IIb]:

$$\begin{aligned} \hat{m}_x &= \hat{m}_y, \\ \hat{V}_{b,x} &= \hat{V}_{w,x} = 0, \\ \hat{V}_{b,y} &= \hat{V}_{w,y} = 0, \\ \hat{Cov}_L &= 0. \end{aligned} \tag{A}$$

or

$$\begin{aligned} \hat{m}_x &= \hat{m}_y, \\ \hat{V}_{b,x} &= \hat{V}_{w,x} = 0, \\ \hat{V}_{b,y} &= \hat{V}_{w,y} = \frac{(\tau - 1)}{\tau} \cdot R_w, \\ \hat{Cov}_L &= 0. \end{aligned} \tag{B}$$

Note that there are additional solutions for  $r_L = 1$ , but iterations using equations [5] suggest that this amount of linkage disequilibrium cannot be stable.

(b) *Dynamics*

Difference equations [5a] and [5b] combine to:

$$\Delta(m_x - m_y) = C(m_x - m_y)$$

For both equilibria [A] and [B]  $m_x$  should equal  $m_y$  which is unstable when  $C > 0$ , implying that:

$$r_L \sqrt{V_{b,x} V_{b,y}} > \frac{\tau}{\tau + 1} V_{b,y} + \frac{1}{\tau + 1} V_{b,x}$$

The dynamics of variances depend on the changes in total variance. The total variance of the male trait will increase when:

$$V_{b,y} < \frac{\tau - 1}{\tau} (R_w + V_{b,x}) - \frac{1}{\tau r_L^2} V_{b,x} \quad (r_L^2 \neq 0)$$

The total variance of the female trait will increase when:

$$V_{b,y} < \frac{\tau - 1}{\tau} (R_w + V_{b,x}) - \frac{r_L^2}{\tau} V_{b,x}$$

Thus, there is a region for the between-individual variances where the total variances of both the male and female trait increase (see also Fig. 2). From the last inequality it can also be concluded that the set of equilibria [A] can never be stable, as any low value of  $V_{b,y}$  will lead to a further increase in the variance of the female trait.

(c) *Simulations*

The system of difference equations is large and rather complex, thus making a full stability analysis exceedingly difficult. Therefore, simulations were carried out using the difference equations to check whether there are hitherto unsuspected dynamic features of the population's dynamics. These simulations were done for several values of  $\tau$  ( $= 1.1, 1.2, 1.5, 2.0, 2.5$ ), with a constant value of  $R_w$  ( $= 100$ ), and eight different starting conditions. (Fixation of  $R_w$  sets the scale of the model). The iterations were started with the averages for the male and female trait set equal:

$$m_x = m_y = 1050$$

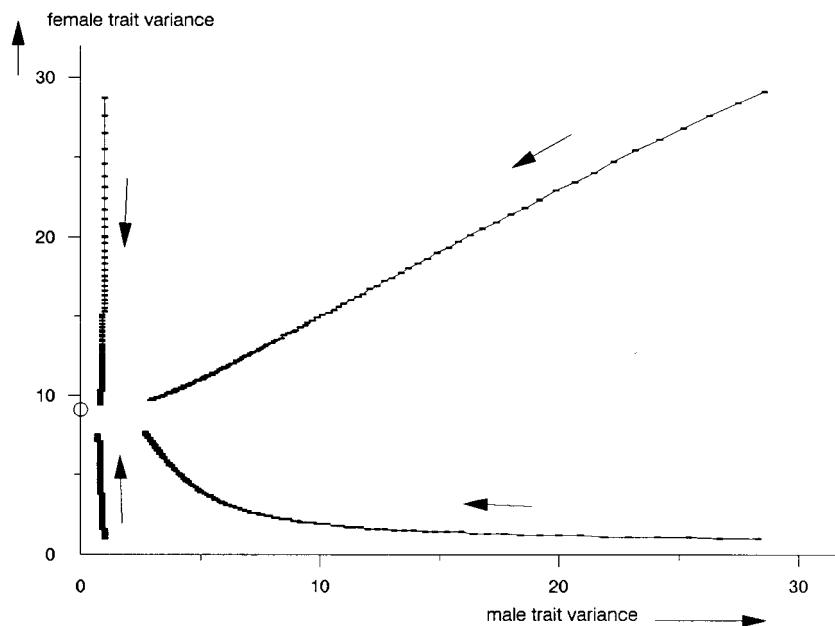
or unequal:

$$m_x = 1000, \quad m_y = 1050$$

These were combined with four combinations for the initial variances, taking the initial covariance equal to zero in all simulations:

- (1)  $V_{b,x} = V_{w,x} = V_{b,y} = V_{w,y} = 0.1$
- (2)  $V_{b,x} = V_{w,x} = V_{b,y} = V_{w,y} = 10.0$
- (3)  $V_{b,x} = V_{w,x} = V_{b,y} = V_{w,y} = 200.0$
- (4)  $V_{b,x} = V_{w,x} = 0.1 \quad V_{b,y} = V_{w,y} = \frac{\tau - 1}{\tau} R_w$

The first three conditions for the variances amount to assuming a random mating population at the start of the simulations, and the fourth condition is an equilibrium near the stable equilibria [B]. These conditions were chosen as they are admissible combinations of the state variables. All these iterations resulted (after 1000 generations) in an approach toward equilibria [B]. Four examples of trajectories through the plane of the between-individual variances are presented in Fig. 3.



**Fig. 3.** Trajectories in the between-individual variance plane for equations [5]. The stable equilibrium is indicated by a circle. Initial conditions  $R_w = 100$ ,  $\tau = 1.1$ ,  $r_L = 0$ , and  $m_x = m_y$ .