SEXUAL SELECTION AT A MULTIALLELIC LOCUS WITH COMPLETE OR PARTIAL DOMINANCE*

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SUMMARY

In this paper we analyse three general models of sexual selection. In one of the models, an ordered series of multiple alleles determines a series of distinct phenotypes in a dominance hierarchy, each phenotype being dominant to all phenotypes below it in the hierarchy. In another model, some alleles determine an ordered hierarchy of dominant phenotypes; others are co-dominant, each genotype producing a separate phenotype except when in combination with one of the dominant alleles. In the third model, two groups of alleles form two separate dominance hierarchies with co-dominance between alleles from each group. In the model with ordered dominance, a unique, globally stable equilibrium is attained at which the frequencies of the phenotypes are exactly proportional to their rates of preferential mating. In the model with dominance and co-dominance, a unique, globally stable equilibrium is also attained. The gene frequencies at equilibrium are given by hybrid expressions combining the frequencies for complete dominance with those for complete co-dominance. An explicit solution is not found when the alleles form two separate dominance hierarchies; but a unique, globally stable equilibrium exists from which the equilibrium frequencies can be obtained by an iterative method. We also analyse some special models with a limited number of alleles and different dominance and co-dominance relationships. In a model with inclusion relationships between the alleles, an allele giving rise to one sexually selected dominant phenotype may also be included with another allele to give rise to a separate sexually selected phenotype. Thus the genotypes A_1A_1 , A_1A_2 and A_1A_3 may represent one sexually selected phenotype; the genotypes A_1A_1 , A_1A_2 , A_1A_3 , A_2A_2 and A_2A_3 may represent another sexually selected phenotype. This is a model of how sexual selection might operate in favour of increasing expression of a character: some females may respond to males with either the alleles A_1 or A_2 ; other females may only respond to males with the more extreme phenotype determined by the allele A_1 . At equilibrium, the allele A_2 will have been eliminated.

1. INTRODUCTION

POLYMORPHISMS in colour patterns are often determined by a series of multiple alleles that can be arranged in a dominance hierarchy in which one allele is dominant or partially dominant to all the others below it in the hierarchy. The following examples represent polymorphisms of this sort: the mimics of the butterflies *Papilio dardanus* and *Papilio memnon* (Sheppard, 1961; Clarke *et al.*, 1968), and *Hypolimnas misippus* (Smith, 1973); melanic and non-melanic forms of the moth *Biston betularia* (Kettlewell, 1973), of the feral pigeon (Murton *et al.*, 1973), and of the ladybird beetle *Adalia bipunctata* (Hodek, 1973; Muggleton, 1978, 1979); shell colours of the snail *Cepaea memoralis* (Cain *et al.*, 1960), and colours and

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shell banding patterns in many other snails. The alleles may often be more or less completely dominant in their effects, but some of the heterozygotes may be distinct phenotypes, as for example in *Papilio dardanus* and *Adalia bipunctata*.

Some of these examples of polymorphisms show the effects of preferential mating. Melanic and non-melanic morphs of the feral pigeon assort negatively at mating: wild-types prefer the melanic morphs *blue checker* and *dark blue checker* (Murton *et al.*, 1973). This observation suggests that wild-type females may prefer to mate with the melanic males. Davis and O'Donald (1976) estimated the levels of female preference by fitting a model of negative assortative mating to the data. Burns (1966) showed that sexual selection may operate between morphs of *Hypolimnas misippus*. Muggleton (1979) and O'Donald and Muggleton (1979) showed that melanic and non-melanic morphs of *Adalia bipunctata* were the objects of strong sexual selection. In *Adalia*, the polymorphism consists of a series of morphs that can be arranged in a series of increasing melanism. The non-melanic morph, which is red with two black spots, is recessive to all the melanic morphs. If the melanics are all linked together in a single class, frequency-dependent sexual selection can then be seen to operate between the melanics and non-melanics: a mating advantage is gained by the rarer phenotype. Preferential mating of melanic and non-melanic phenotypes would produce this frequency-dependence in mating advantage (O'Donald, 1980). The different colours of the male ruff (*Philomachus pugnax*) and guppy (*Poecilia reticulata*) are certainly selected sexually. The different forms of guppies do indeed show the "rare male" effect characteristic of sexual selection by female choice (Farr, 1977). There are other examples of polymorphisms that are probably determined by a series of dominant or partly dominant alleles and maintained by sexual selection.

In theoretical studies of sexual selection for dominant and recessive phenotypes, models have been analysed in which there are only two phenotypes, one dominant to the other (O'Donald, 1963, 1973, 1977, 1978, 1980; Karlin, 1978; Karlin and Raper, 1979; Karlin and Farkash, 1978). In this paper we analyse more general models with multiple alleles. These models are directly applicable to some of the polymorphisms already mentioned. In particular, the polymorphism in *Adalia bipunctata* appears to be maintained by preferential mating of phenotypes determined by a series of at least twelve alleles with a partial dominance hierarchy in which some heterozygotes can be recognised. As well as the general model, in which each allele is dominant to all alleles below it in the hierarchy, we also analyse models with only partial dominance. In models with partial dominance, some heterozygotes are distinct for any homozygote and thus may be subject to separate preferences. These models will certainly be applicable to specific polymorphisms like that of *Adalia* in which dominance may not be complete for all alleles.

In an alternative model (Section 6) with partial dominance, and inclusion relationships, females are more responsive to the more extreme phenotype. Thus, in *Adalia bipunctata*, some females may respond to all melanic phenotypes; others may only respond to the darker or darkest melanics. This mating behaviour would result if the darker melanics provided the greater stimulus so that more females preferred them.

2. THE COMPLETE DOMINANCE ORDERING MODEL

In the sexual selection model for a one locus diallelic trait where allele A is dominant to allele a , there are two phenotypic classes $\bar{A} = \{AA, Aa\}$ and $\{aa\}$, with preferential mating rates α and γ . The rates α and γ refer to the dominant and recessive types specifying the fraction of females, independent of their genotype, that choose males of the respective types. We assume: all females are fertilised, males are polygamous; population sizes are large; and there is a 1:1 sex ratio (cf. O'Donald, 1977; Karlin, 1978). In this framework there exists a unique globally attracting polymorphism at Hardy-Weinberg frequencies with

$$\begin{aligned} p_A &= \text{frequency of allele } A = 1 - \sqrt{\frac{\gamma}{\alpha + \gamma}} \\ p_a &= \text{frequency of allele } a = \sqrt{\frac{\gamma}{\alpha + \gamma}}. \end{aligned} \quad (1)$$

In this study we investigate the extension of this model to a dominance hierarchy of n -alleles. We concentrate first on the case of a complete ordering of dominance and in the following sections some formulations of partial and mixed dominance relationships are considered. The interest and relevance of these models is discussed in the introduction. Some interpretations and implications of our results are provided in the concluding section.

Consider a population of a trait involving n -alleles subject to the dominance ordering

$$A_1 < A_2 < A_3 < \dots < A_n \quad (2)$$

representing n phenotypes, the phenotypic expression depending on the dominant allele. Specifically, the phenotype classes consist of the genotypes as shown:

$$\mathcal{P}_k = \{A_k A_k, A_k A_{k-1}, \dots, A_k A_1\} \quad k = 1, 2, \dots, n. \quad (3)$$

Let the mating preference rate for $\mathcal{P}_k$ be α_k , that is, a fraction α_k , $k = 1, 2, \dots, n$, of all females select a male of phenotype $\mathcal{P}_k$ and the remaining fraction of the female population $1 - \sum_{i=1}^n \alpha_i$ exercise no mating preference, *i.e.*, they choose mates at random from the male population.

It is convenient to introduce the *ordered* genotype frequencies

$$u_{ij} = \text{freq}(A_i A_j) \quad \text{in the female population at the zygote stage,} \quad (4)$$

where the first (second) allele of the genotype A_i (A_j) corresponds to the maternal (paternal) gamete contribution of the preceding generation. Of course, $u_{ij} = u_{ji}$. At the zygote state, the equal sex ratio gives rise to the same genotypic frequencies in males and females.

To ease the later developments we set the notation for the allele frequencies and phenotype frequencies to correspond to (4). Thus

$$\begin{aligned} p_i &= \text{freq}(A_i) \\ &= \sum_{r=1}^n \left(\frac{u_{ir} + u_{ri}}{2} \right) \quad i = 1, 2, \dots, n \end{aligned} \quad (5)$$

and

$$\begin{aligned}\pi_k &= \text{frequency of phenotype } \mathcal{P}_k \\ &= u_{kk} + \sum_{r=1}^{k-1} (u_{kr} + u_{rk}).\end{aligned}\quad (6)$$

In the analyses to follow we rely heavily on the fact established by Karlin (1978, section 7) that for all models of sexual selection in which certain subpopulations of females exercise preferences towards different male phenotypes and which may allow a host of ecological, physiological or behavioural adaptations, the equilibrium frequency configurations are always in Hardy-Weinberg proportions. In particular, this result applies to both monogamous and polygamous bond formation, variation of female response to male behavioural patterns, intensity of male courtship, and natural selection forces operating on the male. The Hardy-Weinberg property for equilibrium states is generally not valid under assortative mating or for regular inbreeding systems.

The recursion relations for the general model reduce to (see Karlin, 1978, equation 7.9)

$$u'_{ij} = \frac{1}{2}[p_i f_j + p_j f_i] \quad (7)$$

where

$$f_i = f_{ii} + \frac{1}{2} \sum_{\substack{r=1 \\ r \neq i}}^n f_{ir} \quad (8)$$

and f_{ij} is the effective male frequency of genotype $A_i A_j$ participating in or responding to sexual selection and random mating propensities and associated behavioural requirements.

In the special case of the n -allele complete dominance model (see (2)), we have

$$f_{ij} = \alpha_j \frac{u_{ij} + u_{ji}}{\pi_j} + \left(1 - \sum_{r=1}^n \alpha_r\right) (u_{ij} + u_{ji}) \quad i < j. \quad (9)$$

Indeed, a proportion α_j of females have prescribed mates in phenotype class $\mathcal{P}_j$. The quantity $(u_{ij} + u_{ji})/\pi_j$ is the fraction of males carrying genotype $A_i A_j$ in the phenotype class $\mathcal{P}_j$.

The fraction $1 - \sum_{r=1}^n \alpha_r$ of females choose mates at random from the male population at large.

The recursion equations connecting allele frequencies over successive generations operating on (7) takes the form

$$p'_j = \frac{1}{2}[p_j + f_j] \quad (10)$$

where f_j is defined in (8). We substitute from (9) to get

$$\begin{aligned}p'_j &= \frac{1}{2} \left[p_j + \alpha_j \left(\sum_{i=1}^j \left(\frac{u_{ij} + u_{ji}}{2} \right) \right) / \pi_j + \sum_{r=j+1}^n \alpha_r \left(\frac{u_{rj} + u_{jr}}{2 \pi_r} \right) p_j + \left(1 - \sum_{i=1}^n \alpha_i \right) p_j \right] \\ &\quad j = 1, 2, \dots, n. \quad (11)\end{aligned}$$

At an equilibrium, $u_{ij}^* = 2p_i^*p_j^*$, $i \neq j$, $u_{ii}^* = p_i^{*2}$ with all $p_i^* > 0$, the equation (11) with some simplification reduces to

$$Lp_j^* = \alpha_j \frac{K_j^*}{K_j^* + K_{j-1}^*} + p_j^* \sum_{r=j+1}^n \frac{\alpha_r}{K_r^* + K_{r-1}^*} \quad j = 1, 2, \dots, n, \quad (12)$$

where $K_j^* = \sum_{i=1}^j p_i^*$ and $K_n^* = 1$, $L = \sum_{i=1}^n \alpha_i$. Solving by backward induction, we obtain

$$Lp_n^* = \frac{\alpha_n}{K_n^* + K_{n-1}^*} = \frac{\alpha_n}{2 - p_n^*} \quad (13)$$

and therefore

$$(1 - p_n^*)^2 = 1 - \frac{\alpha_n}{L} \quad \text{or} \quad p_n^* = 1 - \sqrt{\sum_{i=1}^{n-1} \frac{\alpha_i}{L}}. \quad (14)$$

Using (14) in (12) for the equation $j = n - 1$ gives

$$Lp_{n-1}^* = \alpha_{n-1} \frac{K_{n-1}^*}{K_{n-1}^* + K_{n-2}^*} + p_{n-1}^* Lp_n^*$$

which implies $Lp_{n-1}^* = \alpha_{n-1}/(K_{n-1}^* + K_{n-2}^*)$ and inductively

$$Lp_k^* = \frac{\alpha_k}{K_k^* + K_{k-2}^*} \quad k = 1, 2, \dots, n. \quad (15)$$

The equations can be solved recursively yielding

$$p_k^* = \sqrt{\frac{\sum_{i=1}^k \alpha_i}{\sum_{i=1}^n \alpha_i}} - \sqrt{\frac{\sum_{i=1}^{k-1} \alpha_i}{\sum_{i=1}^n \alpha_i}}, \quad k = 1, 2, \dots, n. \quad (16)$$

Moreover at equilibrium, see (15),

$$(K_r^* + K_{r-1}^*)p_r^* = \pi_r^* = \frac{\alpha_r}{\sum_{i=1}^n \alpha_i} \quad (17)$$

which shows that the phenotype equilibrium frequencies are exactly proportional to the preferential mating rates for the corresponding phenotypes.

The allele frequency levels are marginally of the order of the square root of the $\{\alpha_k\}$ as exhibited in (16). In particular, when $\alpha_1 = \alpha_2 = \dots = \alpha_n$ then $p_k^* = \sqrt{k/n} - \sqrt{(k-1)/n}$, $k = 1, 2, \dots, n$. Thus, for α_i equal, $p_1^* > p_2^* > \dots > p_n^*$.

We may inquire what preference rates correspond to equal equilibrium allele frequencies. This requires the approximate determination $\alpha_k \sim c/(k+1)^2$.

Observe from (16) that in the case $\alpha_{k_0} = 0$ (no special preference for allele A_{k_0}) then $p_{k_0}^* = 0$. This result may have been expected.

3. A MIXED MODEL OF DOMINANCE AND CODOMINANCE

Consider first the sexual selection model of n codominant alleles where each genotype engenders a distinct phenotype. If the mating preference

rate for $A_i A_j$ males is α_{ij} , the unique stable equilibrium has allele frequencies

$$p_i^* = p^*(A_i) = \frac{\alpha_{ii} + \frac{1}{2} \sum_{j=1, j \neq i}^n \alpha_{ij}}{\sum_{k,l} \alpha_{kl}}$$

with corresponding genotype frequencies determined from these allele frequencies in Hardy-Weinberg ratios.

Consider next the hierarchical structure

$$A_n > A_{n-1} > \cdots > A_{k_0} > \left\{ \begin{array}{c} A_{k_0-1} \\ \vdots \\ A_2 \\ A_1 \end{array} \right\}$$

signifying that A_m , $m = n, n-1, \dots, k_0$, are each alleles dominant to alleles of lower indices forming the phenotype grouping

$$\begin{aligned} \mathcal{P}_n &= \{A_n A_n, A_n A_{n-1}, \dots, A_n A_1\} \\ \mathcal{P}_{n-1} &= \{A_{n-1} A_{n-1}, A_{n-1} A_{n-2}, \dots, A_{n-1} A_1\} \\ &\vdots \\ \mathcal{P}_{k_0} &= \{A_{k_0} A_{k_0}, A_{k_0} A_{k_0-1}, \dots, A_{k_0} A_1\} \end{aligned} \quad (18a)$$

while the other genotypes

$$\{A_r A_s\} \quad 1 \leq r \leq s \leq k_0 - 1 \quad (18b)$$

express distinguishable phenotypes. Let

$$\{\alpha_n, \alpha_{n-1}, \dots, \alpha_{k_0}, \gamma_{rs} \quad 1 \leq r \leq s \leq k_0 - 1\} \quad (19)$$

be the preferential mating rates for the various phenotypes. Extending the analysis of the previous section we can establish the following result. The unique stable equilibrium allele frequencies for the phenotype classification of (18) with sexual selection parameters (19) are explicitly given by

$$\begin{aligned} p_n^* &= 1 - \sqrt{\frac{L - \alpha_n}{L}} \\ p_i^* &= \sqrt{\frac{L - \alpha_n - \alpha_{n-1} - \cdots - \alpha_{i+1}}{L}} \\ &\quad - \sqrt{\frac{L - \alpha_n - \alpha_{n-1} - \cdots - \alpha_i}{L}}, \quad k_0 \leq i \leq n-1 \end{aligned} \quad (20a)$$

with $L = \sum_{i=k_0}^n \alpha_i + \sum_{r,s=1}^{k_0-1} \gamma_{rs}$, while

$$p_i^* = \left(\sqrt{\frac{\sum_{r,s=1}^{k_0-1} \gamma_{rs}}{L}} \right) \left(\frac{\gamma_{ii} + \frac{1}{2} \sum_{r=1, r \neq i}^{k_0-1} \gamma_{ri}}{\sum_{r,s=1}^{k_0-1} \gamma_{rs}} \right), \quad i = 1, 2, \dots, k_0. \quad (20b)$$

The genotype frequencies are determined from $\{p_i^*\}$ in Hardy-Weinberg proportions.

In comparing (20) with (16) we find that this model appears to be a hybrid version of the models with complete dominance and with complete codominance. This result is not found when partial dominance patterns do not factorise so simply.

4. MODELS WITH SEPARATE SERIES OF ALLELIC DOMINANCE ORDERINGS

Consider a locus with $n + m$ alleles composed of two all-allelic series

$$A_1 < A_2 < A_3 < \cdots < A_n$$

and

$$B_1 < B_2 < B_3 < \cdots < B_m$$

where the notation indicates that the A alleles form a dominance hierarchy as in section 2 of n phenotype classes

$$\mathcal{P}_k(A) = \{A_k A_k, A_k A_{k-1}, \dots, A_k A_1\}, \quad k = 1, 2, \dots, n \quad (21)$$

and the B alleles form a separate dominance ordering

$$\mathcal{P}_l(B) = \{B_l B_l, B_l B_{l-1}, \dots, B_l B_1\}, \quad l = 1, 2, \dots, m. \quad (22)$$

The genotypes $\{A_i B_j\}$ are assumed to be codominant in phenotypic expression. Suppose the preferential mating rates are

$$\alpha_1, \alpha_2, \dots, \alpha_n \quad \text{with respect to the phenotype classes } \mathcal{P}_k(A),$$

and (23a)

$$\beta_1, \beta_2, \dots, \beta_m \quad \text{for the phenotype classes } \mathcal{P}_l(B).$$

Let the preference rates for the phenotype = genotypes

$$\{A_k B_l\} \text{ be } \gamma_{kl} \quad k = 1, 2, \dots, n, \quad l = 1, 2, \dots, m. \quad (23b)$$

Using the fact that all equilibria exhibit Hardy-Weinberg form, and the general recursion relations (10), we can establish the existence of a unique stable equilibrium. Let p_k^* , $k = 1, 2, \dots, n$, q_l^* , $l = 1, 2, \dots, m$ be the equilibrium allele frequencies.

The individual p_i^* and q_j^* satisfy the equations

$$Lp_i^* = \alpha_i \frac{K_i^*}{K_i^* + K_{i-1}^*} + \left(\sum_{l=i+1}^n \frac{\alpha_l}{K_l^* + K_{l-1}^*} \right) p_i^* + \frac{1}{2} \sum_{j=1}^m \gamma_{ij}, \quad i = 1, 2, \dots, n \quad (24)$$

$$Lq_j^* = \beta_j \frac{L_j^*}{L_j^* + L_{j-1}^*} + \left(\sum_{l=j+1}^m \frac{\beta_l}{L_l^* + L_{l-1}^*} \right) q_j^* + \frac{1}{2} \sum_{i=1}^n \gamma_{ij}, \quad j = 1, 2, \dots, m, \quad (25)$$

where

$$K_i^* = \sum_{\lambda=n-i+1}^n p_\lambda^* \quad \text{and} \quad L_j^* = \sum_{\mu=m-j+1}^m q_\mu^* \quad (26)$$

following the analysis of (12).

We obtain explicitly

$$K_n^* = \sum_{i=1}^n p_i^* = \frac{L_A}{L} = \frac{\sum_{i=1}^n \alpha_i + \frac{1}{2} \sum_{k,l} \gamma_{kl}}{\sum_{i=1}^n \alpha_i + \sum_{j=1}^m \beta_j + \sum_{k,l} \gamma_{kl}} \quad (27)$$

and

$$L_m^* = \sum_{j=1}^m q_j^* = \frac{L_B}{L} = 1 - \frac{L_A}{L} \quad (28)$$

These formulas show that the separate conglomerates of the A and B series of alleles at equilibrium behave as two simple codominant alleles.

We validate the relation (27) as follows. Adding the equations of (24) gives

$$\begin{aligned} LK_n^* &= \sum_{i=1}^n \alpha_i \frac{K_i^*}{K_i^* + K_{i-1}^*} + \sum_{k=1}^n \left(\sum_{l=k+1}^n \frac{\alpha_l}{K_l^* + K_{l-1}^*} \right) p_k^* + \frac{1}{2} \sum_{k,l} \gamma_{kl} \\ &= \sum_{i=1}^n \alpha_i + \frac{1}{2} \sum_{k,l} \gamma_{kl} = L_A. \end{aligned}$$

The equation (24) for $k = n$ in view of (27) reduces to

$$Lp_n^* = \alpha_n \frac{K_n^*}{2K_n^* - p_n^*} + \frac{1}{2} \sum_{j=1}^m \gamma_{nj} \quad (29)$$

with $K_n^* = L_A/L$. This quadratic in $p_n^* = p$, namely

$$Lp^2 - \left(2K_n^*L + \frac{1}{2} \sum_{j=1}^m \gamma_{nj} \right) p = - \left(\alpha_n + \sum_{j=1}^m \gamma_{nj} \right) K_n^*$$

admits a unique positive solution. Once p_n^* is determined, then K_{n-1}^* is known and the equation (24) for $k = n-1$ can be used to solve for p_{n-1}^* again from a quadratic equation. This procedure can be iterated to calculate all p_k^* . In a similar manner the values q_i^* are uniquely determined.

The results can be generalized to a multiallelic model comprised of r -dominance series. Indeed, suppose the i th allelic group obeys a dominance ordering

$$A_1^{(i)} < A_2^{(i)} < \dots < A_{n_i}^{(i)} \quad i = 1, 2, \dots, r$$

with codominance phenotypic expression between alleles of different series. Let the preference rates for the dominance class of $A_\lambda^{(i)}$ be

$$\alpha_\lambda^{(i)} \quad \lambda = 1, 2, \dots, n_i; \quad i = 1, 2, \dots, r$$

and $\gamma_{k,l}^{(i,j)}$ the preference mating rate for genotype $\{A_k^{(i)} A_l^{(j)}\}$ for $i \neq j$.

For the foregoing sexual selection random mating model there exists a unique stable Hardy-Weinberg equilibrium array with allele frequencies $\hat{p}_\lambda^{(i)} = \text{freq}(A_\lambda^{(i)})$ constrained to satisfy

$$\hat{K}^{(i)} = \sum_{\lambda=1}^{n_i} \hat{p}_\lambda^{(i)} = \frac{\sum_{\lambda=1}^{n_i} \alpha_\lambda^{(i)} + \frac{1}{2} \sum_{k,l,j} \gamma_{k,l}^{(i,j)}}{\sum_{i,\lambda} \alpha_\lambda^{(i)} + \sum_{i,j,k,l} \gamma_{k,l}^{(i,j)}}.$$

The individual $\hat{p}_\lambda^{(i)}$ can be computed recursively as the roots of appropriate quadratic polynomials.

5. SOME SPECIAL MODELS

Consider the three allele model with phenotypes

	$\{A_1A_1, A_1A_2\}$	$\{A_1A_3\}$	$\{A_2A_2\}$	$\{A_2A_3\}$	$\{A_3A_3\}$	
preferential mating rates	α	γ_1	β	γ_2	γ_3	(30)

There exists a unique stable Hardy-Weinberg equilibrium and the allele frequencies can be explicitly determined as solutions of appropriate quadratic equations (see below).

In fact, the model (30) has A_1 dominant to A_2 and all other genotypes codominants. The equilibrium equations are

$$p_3 = \gamma_3 + \frac{\gamma_1 + \gamma_2}{2} + (1-L)p_3$$

$$p_2 = \frac{\alpha p_2}{p_1 + 2p_2} + \beta + \frac{\gamma_2}{2} + (1-L)p_2$$

$$p_1 = \frac{\alpha p_1 + p_2}{p_1 + 2p_2} + \frac{\gamma_1}{2} + (1-L)p_1.$$

The unique solution (abbreviating $L = \alpha + \beta + \gamma_1 + \gamma_2 + \gamma_3$) has

$$p_3^* = \frac{\gamma_3 + (\gamma_1 + \gamma_2)/2}{L}$$

$$p_2^* = \left(-\frac{(\gamma_1 + \gamma_2 + \beta)}{2} + \sqrt{\left(\frac{\gamma_1 + \gamma_2 + \beta}{2} \right)^2 + 2(\beta + \gamma_2)(1 - p_3^*)L} \right) / 2L$$

$$p_1^* = 1 - p_1^* - p_2^*.$$

The phenotype grouping of nontransitive dominance relationships

	$\{A_1A_1, A_1A_2\}$	$\{A_2A_2, A_2A_3\}$	$\{A_1A_3, A_3A_3\}$
sexual selection rates	α	β	γ

also admits a globally stable equilibrium.

In contrast, the phenotype grouping

	$\{A_1A_1, A_2A_2\}$	$\{A_1A_2\}$
mating sexual selection rates	α	β

which cannot be interpreted in terms of a dominance relationship, can involve multiple stable (Hardy-Weinberg) equilibria for certain ranges of the α, β parameters (see Karlin and Farkash, 1978, table IV).

It appears that with n -alleles with phenotype classes determined by partial dominance relations, a unique stable equilibrium exists subject to sexual selection and random mating forces, but this is not the case with phenotype classes determined by genotype groupings not characterized by dominance ordering.

6. PHENOTYPE CLASSES WITH INCLUSION RELATIONSHIPS

It is illuminating to begin with the following three allele model. Consider three phenotypes

$$\begin{aligned}\mathcal{P}_1 &= \{A_1A_1, A_1A_2, A_1A_3\} = \text{the dominant class of } A_1, \\ \mathcal{P}_{1,2} &= \{A_1A_1, A_1A_2, A_1A_3, A_2A_2, A_2A_3\} = \text{the combined} \\ &\quad \text{dominance group determined by alleles } A_1 \text{ and } A_2, \\ \mathcal{P}_3 &= \{A_3A_3\}.\end{aligned}\quad (31)$$

Suppose the preferential mating rates for the above phenotypes are α , β and γ , respectively. Thus, a fraction α of females prefers the $\mathcal{P}_1$ phenotype, but a different subpopulation, a fraction β of females, favours any genotype carrying either the A_1 or the A_2 allele. Let p_1 , p_2 , and p_3 be the frequencies of the A_1 , A_2 and A_3 alleles, respectively. Appealing to the general sexual selection theory (see especially Karlin, 1978, section 7) the equilibrium equations (since the genotype frequencies are necessarily of Hardy-Weinberg form) reduce to

$$Lp_1 = \alpha \frac{1}{p_1 + 2p_2 + 2p_3} + \beta \frac{p_1}{1 - p_3^2} \quad (32)$$

$$Lp_2 = \alpha \frac{p_2}{1 + p_2 + p_3} + \beta \frac{p_2}{1 - p_3^2} \quad (33)$$

where $L = \alpha + \beta + \gamma$.

Assuming $p_2 > 0$ and cancelling this factor in (32) yields

$$L = \alpha \frac{1}{1 + p_2 + p_3} + \frac{\beta}{1 - p_3^2}. \quad (34)$$

Substituting this expression into (32) and simplifying leads to the equation

$$L(1 - p_1) = \frac{\beta}{1 - p_3^2}(1 - p_1). \quad (35)$$

If $p_1 < 1$, we find that $L = \beta/(1 - p_3^2)$ which in comparison with (34) for $\alpha > 0$ is impossible. The case of $p_1 = 1$ (fixation of only A_1A_1 -genotypes) cannot be stable with some initial representation of allele A_3 when $\gamma > 0$. Thus, the only consistent conclusion has $p_2 = 0$, i.e., allele A_2 cannot be maintained under the sexual selection system of (31) for the phenotype classes $\mathcal{P}_1$, $\mathcal{P}_{1,2}$ and $\mathcal{P}_3$. This is, *a priori*, perhaps surprising in view of the existence of some *a priori* positive preference for phenotype $\mathcal{P}_{1,2}$, which includes some genotypes involving allele A_2 . The intuition after the fact is that, although some fraction among the females indifferently favour the genotypes carrying allele A_2 and A_1 , there are additional females only willing to accept matings with the dominance class of $\{A_1\}$ thereby inducing a uniform advantage for allele A_1 over allele A_2 ; concomitantly allele A_2 cannot be maintained.

The foregoing model suggests a mechanism where the lowest dominant allele A_3 and the highest dominant allele A_1 are represented with moderate frequency while the intermediate allele A_2 barely occurs. Actually, there are such documented examples (e.g. Feral pigeon) where the sexual selec-

tion process coupled to an approximate dominance pattern provides a mechanism of this U-shaped frequency pattern.

The above example is subsumed by the following general formulation. Consider an n allele sexual selection system of possible alleles A_i ($i = 1, 2, \dots, n$) based on a dominance ordering $A_1 < A_2 < \dots < A_n$ which entail the phenotype classes

$$\{A_1\}, \left\{ \begin{matrix} A_2 \\ A_3 \end{matrix} \right\}, \{A_3\}, \left\{ \begin{matrix} A_4 \\ A_5 \\ A_6 \end{matrix} \right\}, \{A_6\}, \dots, \{A_n\} \quad (36)$$

where the symbols are to be interpreted as follows. The phenotype class $\mathcal{P}_n$ consists of all genotypes carrying allele A_n . The phenotype expression of $\mathcal{P}_{n-1}, \dots, \mathcal{P}_6$ is also characterized in a similar manner;

$$\left\{ \begin{matrix} A_4 \\ A_5 \\ A_6 \end{matrix} \right\} \approx \mathcal{P}_{4,5,6}$$

refers to the collection of all genotypes carrying alleles A_4 and/or A_5 and/or A_6 , and $\mathcal{P}_{2,3}$ stands for the genotypes involving alleles A_2 and/or A_3 . Now suppose there is *positive a-priori mating* preference of some fraction of females for each of the male phenotype classes of (36). Then any stable equilibrium necessarily has $p_2^* = 0$ and $p_4^* = p_5^* = 0$. Thus, even though there is some mating preference for $\mathcal{P}_{4,5,6}$ and $\mathcal{P}_{2,3}$ the special preference for $\mathcal{P}_6$ precludes the existence of alleles A_5 and A_4 in evolution. Allele A_2 also cannot be maintained under the phenotype classification (36).

Biologically, this is a realistic model of how preferences might operate to favour increasing levels of expression of a male characteristic. In this general tendency to express a preference, some females will be more responsive than others. In the model specified by (36) above, for example, the more responsive females may prefer males who possess the alleles A_1 or A_2 : they choose to mate with any male who is A_1A_1 , A_1A_2 , A_1A_3 , A_2A_2 , A_2A_3 , A_3A_3 , etc. But the less responsive females may only respond to males in whom the character is more highly developed: these females choose only the A_1A_1 , A_1A_2 or A_1A_3 males.

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