Characterization and Analysis of Mating Systems

HANS-ROLF GREGORIUS

Institut für Forstgenetik und Forstpflanzenzüchtung
Georg-August-Universität Göttingen
Büsgenweg 2, 37077 Göttingen

First printing 1989
Ekopan Verlag, Witzenhausen

Reproduced with permission for distribution under URL
http://webdoc.sub.gwdg.de/ebook/y/2001/gregorius/matesys.pdf

Gregorius, Hans-Rolf. *Characterization and Analysis of Mating Systems.* First printing 1989 by Ekopan Verlag, Witzenhausen, Germany, ISBN 3-927080-05-5.

Reproduced in February, 2001, with permission of the publisher for distribution as an electronic book by the Niedersächsische Staats- und Universitätsbibliothek Göttingen.

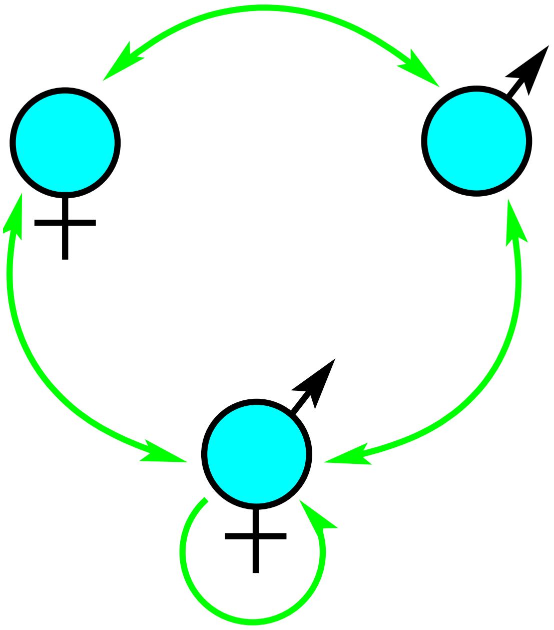
Downloadable as a PDF-file under the URL
http://webdoc.sub.gwdg.de/ebook/y/2001/gregorius/matesys.pdf

Table of Contents

Preliminary Remarks

The consideration of mating systems is meaningful only in connection with sexually reproducing organisms. Sexuality is a very common means of reproduction, and it can take quite diverse forms. Among the most important is **gamogony**, in which specially formed reproductive cells (gametes) fuse (plasmo- and karyogamy). The gametes possess a bipolar differentiation and are termed male and female, according to whether they can be assigned a donor or receptor function, respectively.

Individuals which produce gametes of only one polarity (only female or only male) are called **unisexual**. If gametes of both polarities (female and male) are produced, one speaks of **cosexual** individuals. One can thus distinguish between three **sexual types** (sexes, genders) on the level of *the individual*: two unisexual – a female (denoted by ♀) and a male (♂) – and a cosexual (⚥). Since reproduction is bound to the fusion of a female with a male gamete, cosexual individuals are fundamentally capable of reproducing with each other as well as with unisexual partners. On the contrary, unisexual individuals always require a partner of a different sex (♀ is capable of reproducing with ♂ and ⚥, ♂ with ♀ and ⚥). The sexual compatibility relationships between the three sexual types can be diagrammed as follows:



Cosexuality can arise in very different ways. In both plants and animals, individuals may pass through two unisexual phases of different polarity, in which case they are termed **consecutive cosexual** ('protandrous' if male gametes mature before the female gametes; in the opposite case 'protogynous'). **Simultaneous cosexuality** is realized whenever female and male gametes are produced simultaneously. Dependent on the sex of the flowers, in higher plants differentiation is made between hermaphroditic (all flowers are monoclinous, i.e. produce both female and male gametes), monoecious (separate female – pistillate – and male – staminate – flowers), andromonoecious (male and hermaphroditic flowers), gynomonoecious (female and hermaphroditic flowers), and trimonoecious (female, male, and hermaphroditic flowers) individuals.

The distribution of the sexes in a *population* characterizes its **sexual system**. In accordance with the sexual types present in a population, the following basic systems of sexuality are distinguished: **Cosexuality** (all members of the population are cosexual), **dioecy** (all members are unisexual female or male), **androdioecy** (male and cosexual sexual types), **gynodioecy** (female and cosexual types), and **trioecy** (all three sexual types). However, if a population has cosexual members, such a discrete characterization of its sexual system is often not possible. This is because the two sexual functions of a cosexual individual can differ in proportion, so that a continuum of sexual functions reaching from pure femaleness to pure maleness may occur (cf. Hattemer and Bergmann 1987, p.119f). Among the above-mentioned sexual systems, only dioecy lacks cosexual individuals and thus unambiguously allows a discrete characterization.

In any case, the sexual system sets the limits for the possibilities of mating, e.g. in that unisexual individuals of the same sex cannot successfully mate with each other. The characterization of a mating system must therefore include a description of the sexual system of the population. In addition, it must specify further qualitative and quantitative features directly related to the performance of matings. However, it is often difficult to unambiguously define a mating or its performance, either because the opportunities for observation are limited or since different goals may necessitate different descriptions. For the sake of generality, it is therefore advisable to agree upon the smallest common denominator by regarding **mating** only as *binary relation* between individuals. The concept of the individual can refer here to either the diplophase or the haplophase. In higher animals, for example, where mating is frequently considered as copulation or internal fertilization, the individuals involved are usually in the diplophase. In the case of external fertilization, as is characteristic of most plant species, it can be appropriate to define a **mating event** as the fusion of two gametes and to regard these gametes as the (haplophase) individuals undergoing mating. The search for gametophytic incompatibility, where the formation of a zygote is determined by properties of both the (diploid) pistil and the (haploid) pollen, can even make it necessary to regard the formation of mating pairs as between diplo- and haplophase individuals.

For reasons of gradual accumulation of knowledge and perception, it is frequently of particular interest to consider mating on several levels. As already mentioned, the performance of mating e.g. in wind-pollinated, cosexual plants is usually considered on the level of the gametes. However, identification of each gamete with its producer allows the mating to be traced back to the diplophase level. Due to individual differences in the production of ovules and pollen (fertilities), quite different characterizations of the mating system can result, according to which of the two levels is regarded. These statements apply analogously to dioecious animals. However, in this case the focus is primarily on the diplophase, and a characterization of the haplophase must account for the fact that the fecundity of the single (diplophase) pairs may vary.

These examples illustrate two important aspects of the concept of mating systems: (a) Counting of mating events must be based on an unambiguous definition of the concept of mating, which can, however, depend on the respective objective; (b) the characterization and classification of mating systems essentially depends on which individuals are viewed as potential mating partners and thus as mating reference. Each description of the circumstances of mating must therefore be based on a comparison between the actually performed and the potential matings. The most basic objective of such a comparison consists in deriving a qualitative and quantitative specification of mating preferences. This applies equally to experimental and theoretical investigations which differ only in that the first is primarily concerned with the detection of mating preferences and the latter with their generation by means of analysis of special models and their parameters.

The main objective of the present treatise lies in the presentation of a consistent and widely applicable formulation of the above-mentioned basic terms (mating, mating reference, mating preference). This definition of terms serves as the basis for the attempt to construct a formal biological characterization and classification of mating systems, at the same time providing an Ansatz for the derivation of appropriate methods of analysis. The applicability for the interpretation of experimental data will be demonstrated with the help of examples. However, the analysis of phenotypic and genotypic models and their integration into the conception of mating systems presented here will receive the most attention. Most of the models treated are of a new kind; nevertheless, due to the generality of the parameterization, they include a wide range of model types dealt with in the relevant technical literature.

A further aspect which is treated in more detail is differential mating success, which arises as a consequence of particular mating systems. This aspect introduces an additional criterion for characterization. Particularly in studies in population genetics and evolutionary biology, this aspect possesses central importance. The measurement of mating success in the sense of reproductive success is immediately related to the concept of fitness and thus to the principle of "survival of the fittest". Yet this is meaningful only when viewed together with particular modes of inheritance: in general, reproductive superiority of a type does not necessarily imply its evolutionary superiority. This phenomenon will also be demonstrated with the help of several model examples.

In view of the overwhelming profusion of problems which are treated in the technical literature under the topic "mating systems", the author decided to refrain to a possibly unusual extent from a representative citation in order to concentrate on the presentation of the subject. The objectives are mainly of a conceptual nature, and the presented results should merely be understood as an indication of the possibilities that emanate from a consistent application of the recommended notions and methods of characterization.

The author is greatly indebted to E. Gillet, M. Häcker, H.H. Hattemer and M. Ziehe for their continual willingness to engage in discussions. The computational analyses of the models were made possible by a "Kleinförderung" of the Deutsche Forschungsgemeinschaft.

1. Formal description of mating systems

Consider any population each individual member of which is classified by a set of properties which serve to characterize its **type**. The different types present in the population will be denoted by $T_1, T_2, T_3, \ldots$. For convenience only, this typification is assumed to be denumerable. Among the very diverse properties that can characterize a type are phenotypic traits, such as sexual type, genetic traits, age, ecological conditions to which the members are exposed, or even the location at which they reside during certain periods of time. Genealogical traits can also be of interest, although they are usually specified as consanguinity relationships within pairs of individuals. However, even each single individual can be typified in genealogical terms independently of others by regarding all individuals having a particular ancestry in common as representatives of the same type. Thus, two individuals belong to different (genealogical) types if they differ in the ancestors used for typification.

A mating between an individual of type T_i and a second individual of type T_j is represented by the symbol $T_i \times T_j$, where $T_i \times T_j$ is called the **mating type** of this mating event. It has to be noticed that among cosexual organisms matings of the type $T_i \times T_i$ include the possibility of individual self-fertilization. For the sake of simplicity, it will, for the time being, be assumed that the number of matings performed in a population is finite. Under this assumption the following absolute frequencies are meaningful:

Notations

$K(T_i \times T_j) :=$ number of matings of the type $T_i \times T_j$;

$K :=$ $\sum_{i\leq j} K(T_i{\times}T_j)$, or total number of matings performed in the population;

$K_i :=$ frequency with which T_i-individuals participate in all matings performed in the population (**mating participation** *of the type* T_i*).*

When computing the frequencies K_i it must be considered that, whereas T_i-individuals appear only once in matings of the type $T_i \times T_j$,

$i \neq j$, while they appear twice in matings of the type $T_i \times T_i$. One thus obtains

$$K_i = \sum_{j,j\neq i} K(T_i \times T_j) + 2 \cdot K(T_i \times T_i)$$

and, therefore,

$$\sum_i K_i = 2 \cdot K.$$

These are the fundamental quantities that result from counting single matings in each experiment. The pertinent relative frequencies are

Notations

$P(T_i \times T_j) :=$ $K(T_i \times T_j)/K$, or the relative frequency of matings of the type $T_i \times T_j$ among all matings performed in the population;

$P(T_i) :=$ $K_i/(2 \cdot K) = \sum_j \frac{1}{2}(1+\delta_{ij}) \cdot P(T_i \times T_j)$, or the relative frequency with which T_i-individuals appear among all matings.

Here δ_{ij} denotes the so called "Kronecker delta", i.e. $\delta_{ij} = 0$ for $i \neq j$ and $\delta_{ii} = 1$. The set of relative frequencies (or probabilities in populations of hypothetically infinite size) $P(T_i \times T_j)$ will be called **mating frequencies** in the sequel.

As will become more evident later, it is desirable to relate the mating frequencies not to all matings performed in the population but rather to the frequency with which a particular type participates in the matings. For a given type one thus considers the frequencies with which it engages in matings with other types and with its own type:

Notations

$P_{j\triangleleft i} :=$ relative frequency with which T_j-individuals appear among all matings performed by T_i-individuals.

Consequently, $\sum_j P_{j\triangleleft i} = 1$ for all i, and it follows immediately that

$$P_{j\triangleleft i} = \frac{\frac{1}{2}(1+\delta_{ij}) \cdot P(T_i \times T_j)}{P(T_i)} \,. \tag{1.1}$$

The $P_{j \lhd i}$'s correspond to the conditional probabilities known from probability theory, since the following equations hold:

$$P_{j \lhd i} \cdot P(T_i) = P_{i \lhd j} \cdot P(T_j) \quad \text{and} \quad \sum_j P_{i \lhd j} \cdot P(T_j) = P(T_i). \qquad (1.2)$$

However, unless the types involved in a mating $T_i \times T_j$ have a pre-assigned order, the sample space consisting of the mating types $T_i \times T_j$ cannot, in general, be represented as the Cartesian product of two marginal spaces. Such an order can be specified in a natural manner for dioecious species, in which male and female individuals can be distinguished, but no biologically meaningful order can be assigned in cosexual or trioecious populations, for example. As was pointed out earlier, sex should be included as one of the attributes characterizing the type of an individual, and it is, therefore, not necessary to assign any specific ordering relationship to the mating types. Moreover, this helps to avoid arbitrariness and ambiguity in the representations.

In order to distinguish them from the mating frequencies, the set of $P_{j \lhd i}$'s will be called the **mating norm**. The mating norms are completely determined by the mating frequencies, if all $P(T_i)$'s are positive. Yet, in the reverse direction, given the mating norms, the mating frequencies are in general not uniquely determined whenever certain of the $P_{j \lhd i}$'s are equal to 0. This is the case, for example, when for two types $P_{2 \lhd 1} = P_{1 \lhd 2} = 0$ and $P_{1 \lhd 1} = P_{2 \lhd 2} = 1$ hold.

1.1 Mating references (potential mating partners)

When describing the system according to which individuals mate, in addition to the actual mating frequencies, information about the potential mating partners that are or could be available is required. Only the comparison between the actually performed and the potential matings can lead to the discovery of laws governing the performance of matings. In general, the composition of the group of potential mating partners of a particular type may differ from that of another type in kind as well as in frequency distribution of the types in the groups. The following quantities are thus fundamental for any description of a mating system:

Notations

$R_{j\triangleleft i}$:= relative frequency of the type T_j among the potential mating partners of T_i-individuals ($\sum_j R_{j\triangleleft i} = 1$).

Each set of conditional frequencies $R_{j\triangleleft i}$ allowing for the above interpretation will be called a **mating reference**.

At least in principle, it is possible to choose different mating references for a single population with its given mating frequencies. This choice will depend on the respective objective as well as on the information available. For example, in a dioecious population it may be meaningful to assume for all female types the same mating reference consisting of all males. Since the sexual type determines the opportunities for mating between individuals in a fundamental manner, this situation may even be conceived of as a “natural” mating reference. On the other hand, if, for example, additional information is available about the sexual maturity of the single individuals, this could enter into the typification as an additional criterion, and would thus possibly lead to different mating references for the respective female type. Similar situations could arise with other sexual systems, including a large number of incompatibility systems. In any case, the more information on the opportunities for mating, the closer the mating reference can be chosen to approach the mating frequencies or the mating norm. In the extreme case, which is however only of theoretical relevance, this would result in identity of the mating reference and the mating norm, i.e. $R_{j\triangleleft i} = P_{j\triangleleft i}$ for all mating types.

The constructive specification of a mating system, i.e. the rules or laws according to which the mating norm results from the mating reference, can, in general, not be uniquely specified, since in most cases the actual causes for the mating behaviour cannot be inferred and must therefore be replaced or supplemented by assumptions. Beyond this, there are usually many ways to compare mating norms and mating references, so that the following definition possesses wide applicability:

Definition

In an operational definition a mating system consists of the mating reference and the mating norm. Both refer to particular properties (types) of the members of a population.

A characterization of a mating system which is based solely on observations of mating norms or mating frequencies and does not consider mating references is, therefore, without meaning. This has to be remembered when data on potential mating partners cannot be obtained because of technical or experimental problems in the experimental design.

1.2 Mating preferences

Usually, the first step in the characterization of a mating system consists in posing the question as to whether the members of the population mate at random with respect to the trait (the types) under consideration. If they do not, one commonly speaks of **preferential mating** among at least some of the types represented in the population. This, of course, requires specification of potential mating partners (and thus the mating reference) with respect to which the presence or absence as well as the pattern of preferential mating are to be stated. Since each type may differ from each other in its mating preferences, it is necessary to consider its mating norm separately, and to compare it with the pertinent mating reference. Thus, the mating preferences of a type T_i result from the comparison of the $P_{j\lhd i}$'s with the $R_{j\lhd i}$'s for $j = 1, 2, 3, \ldots$. The probably most direct method of comparison consists in the computation of the number of matings performed by T_i-individuals with T_j-individuals per potential mating of this type. The total number of matings performed by T_i-individuals is given by K_i, and out of this number a fraction $P_{j\lhd i}$ is due to actual matings and a fraction $R_{j\lhd i}$ to potential matings of the type $T_i \times T_j$. Thus, the ratio between actual and potential matings which T_i-individuals perform with T_j-individuals is given by $P_{j\lhd i} \cdot K_i / (R_{j\lhd i} \cdot K_i)$. This ratio will be called the **mating preference** *of the type T_i for the type T_j*, and it will be symbolized by

$$U_{j\lhd i} := \frac{P_{j\lhd i}}{R_{j\lhd i}} \ .$$

The $U_{j\lhd i}$'s are defined only for $R_{j\lhd i} \neq 0$, and this is is also the only relevant case, since $R_{j\lhd i} = 0$ must always imply $P_{j\lhd i} = 0$.

Random mating is conceived of as the absence of mating preferences. This is equivalent to the situation where the types mate with each other according to their frequencies among the potential mating partners, i.e. $P_{j\lhd i} = R_{j\lhd i}$ and thus $U_{j\lhd i} = 1$. If this holds true for all mating types

$T_i \times T_j$ with $R_{j\lhd i} \neq 0$, then we are used to speaking of a **random mating population**. However, random mating need not be realized for all types in a population, in which case some of the U's are expected to be equal to 1 but others are not. If for a particular type T_i, say, all its U-values are equal to 1, i.e. $U_{1\lhd i} = U_{2\lhd i} = \ldots = 1$, then this type can be said to mate at random with the whole population. On the other hand, it is also conceivable that a type T_i mates at random with some but not with other types. This case would be characterized, for example, by $U_{j\lhd i} = 1$ and $U_{k\lhd i} \neq 1$ for $j \neq k$. It is therefore meaningful to base the definition of random mating on single mating types, so that $U_{j\lhd i} = 1$ means "type T_i mates at random with type T_j". In general this statement does not hold in the reverse direction, i.e. random mating of T_i with T_j need not imply random mating of T_j with T_i. In other words, mating preferences may be asymmetrical in the sense that $U_{j\lhd i} \neq U_{i\lhd j}$ can hold.

Preferential mating may occur in two fundamentally different forms, namely positive preferential mating with $U_{j\lhd i} > 1$ (T_i has a positive preference for T_j) and negative preferential mating with $U_{j\lhd i} < 1$ (T_i has a negative preference for T_j). Since $\sum_j U_{j\lhd i} \cdot R_{j\lhd i} = 1$ always holds, a type might either show no preferences at all, i.e. it mates at random with the whole population, or it must have negative as well as positive mating preferences. These notions should not be confused with those of positive and negative assortative mating. The latter refer to mating preferences that arise from similarity or dissimilarity between the mating partners. As expressed with the help of the U-values, **positive assortative mating** would yield $U > 1$ and **negative assortative mating** $U < 1$ for matings between phenotypically similar individuals. Hence the notions positive and negative assortative mating are meaningless, unless it is possible to draw similarity relationships between the types. This is the case, for example, if in dioecious populations the two sexes are characterized by different traits (sex-specific traits).

1.3 Mating success

The extent to which an individual participates in the mating process is described by the number of matings it performs. Let w_i be the average number of matings performed by a T_i-individual, and let $\bar{w}$ be the number of matings performed by an average individual from the total population. Moreover, since for a particular population the participation of a type in the mating process is meaningful only with respect to the population average, the mating success of T_i-individuals is defined by $h_i := w_i/\bar{w}$. Consequently, letting N be the population size and Q_i the relative frequency of T_i-individuals, one obtains $w_i = K_i/(N \cdot Q_i)$ and $\bar{w} = \sum_i w_i \cdot Q_i = 2K/N$. Hence, the **mating success** *of T_i-individuals* is given by

$$h_i = \frac{P(T_i)}{Q_i} \tag{1.3}$$

Mating success can be equated to relative Darwinian fitness, if the Q_i's are referred to the zygotic stage and a mating is declared to be the fusion of gametes. In this situation w_i is the average number of successful gametes (that is, gametes entering into zygotes) and $\frac{1}{2}\bar{w}$ is the population fitness. Therefore, the mating success can be conceived of as a generalization of the concept of relative fitness, where the successful gametes are to be identified with the mating participation and where the evaluation of the frequencies of the types is not restricted to a particular ontogenetic stage.

The fact that, in general, the frequencies Q_i of the types T_i need not be directly related to the mating reference shows that the mating success also need not be directly associated with the mating system. *Only if the mating reference is chosen in accordance with the frequencies of the types in the population, is it possible to study the effects of mating systems on mating success.*

1.4 Conditional random mating

As already discussed in Section 1.2, a type can mate at random with some of its potential mating partners but need not do so with all of them. This situation was characterized by $U = 1$ for the former. There is an additional possibility for such restricted random mating, which does not even necessarily result in mating preferences $U = 1$. This possibility reflects the situation where a type discriminates between some but not between others of its potential mating partners. Such a type would thus show the same preferences for all types within the group of types among which it cannot discriminate. Suppose that $\mathcal{Z}$ denotes a set of types among which a type T_i does not discriminate with respect to mating. The notation $j \in \mathcal{Z}$ indicates that the type T_j belongs to $\mathcal{Z}$. With this notation

$$P_{\mathcal{Z}\lhd i} := \sum_{j\in\mathcal{Z}} P_{j\lhd i} \quad \text{and} \quad R_{\mathcal{Z}\lhd i} = \sum_{j\in\mathcal{Z}} R_{j\lhd i}$$

are the relative frequencies with which individuals from the group $\mathcal{Z}$ appear among all matings and among all potential mating partners, respectively, of the type T_i.

Considering the mating behaviour of T_i-individuals belonging to the group $\mathcal{Z}$, it follows that for each $j \in \mathcal{Z}$ the conditional mating norm is $P_{j \lhd i}/P_{\mathcal{Z} \lhd i}$ and the conditional mating reference is $R_{j \lhd i}/R_{\mathcal{Z} \lhd i}$. Consequently, the absence of mating preferences and thus **conditional random mating** of T_i-individuals with individuals belonging to the group $\mathcal{Z}$ is equivalent to $P_{j \lhd i}/P_{\mathcal{Z} \lhd i} = R_{j \lhd i}/R_{\mathcal{Z} \lhd i}$ for all $j \in \mathcal{Z}$. Therefore,

$$U_{j \lhd i} = \frac{P_{\mathcal{Z} \lhd i}}{R_{\mathcal{Z} \lhd i}} \quad \text{for all} \quad j \in \mathcal{Z}.$$

In other words, the mating preferences of the type T_i are identical for all types belonging to the group $\mathcal{Z}$, but they need not be equal to 1. On the other hand, if one observes for a type T_i that its mating preferences $U_{j \lhd i}$ are all identical, provided the T_j belong to a particular set $\mathcal{Z}$ $(j \in \mathcal{Z})$, then it follows immediately that the type T_i performs conditional random mating with individuals of the group $\mathcal{Z}$.

Result

A type T_i mates in a conditionally random manner with all types belonging to a set $\mathcal{Z}$ if and only if the mating preferences $U_{j \lhd i}$ assume the same value for all $j \in \mathcal{Z}$.

Simple situations of conditional random mating can arise, for example, if mating is exclusively determined by the time of sexual maturity and if the trait observed is correlated with sexual maturity. Indiscriminate mating is possible among all those individuals that are sexually mature during the same period of time, while other matings would be entirely inhibited.

1.5 Mating equivalence

The characterization of a mating system is always specific for given traits and the thus defined types. Yet, differences between types need not be associated with differential mating behaviour. Individuals of different types can even be completely equivalent in mating behaviour, since this behaviour can be determined by another trait they have in common, but which happens not to be observed or is not even observable. This equivalence must comprise both the propensity for self-mating of single individuals (such as self-fertilization in monoecious plants) and the propensity for cross-mating between individuals of the same or different types. Therefore, each type has to be distinguished with respect to its individual self- and cross-matings. The extent of individual self-mating, i.e. the **proportion of self-mating** of a type T_i, is denoted by

Notations

P_i^s := relative frequency with which self-matings occur among all matings performed by T_i-individuals.

Hence, equivalence of two types T_1 and T_2 with respect to self-mating means that $P_1^s = P_2^s$.

The circumstances of mating among cross-matings will be symbolized by the *cross-mating norms* $P_{i \lhd j}^c$ and by the *cross-mating reference* $R_{i \lhd j}^c$. Here, $P_{i \lhd j}^c$ is the relative frequency with which T_i-individuals occur among all cross-matings performed by T_j-individuals ($\sum_i P_{i \lhd j}^c = 1$). In like manner, $R_{i \lhd j}^c$ denotes the frequency of T_i-individuals among the potential cross-mating partners of T_j-individuals. Thus, the *cross-mating preferences* are given by $U_{i \lhd j}^c = P_{i \lhd j}^c / R_{i \lhd j}^c$. Since the mating behaviour of a type is always characterized only with reference to its potential mating partners, the equivalence of two types with respect to cross-mating is only recognizable by the equality of their cross-mating preferences. It must be kept in mind that this equivalence comprises cross-matings between the two types as well as between either one of the types and a third type (the third can, of course, be one of the initial two). In accordance with the previous section 1.4, this implies conditional random cross-mating with the two types. The complete absence of differences in mating behaviour between two types, i.e. their **mating equivalence**, comprises their self- and their cross-matings, so that the above considerations imply the result stated in the following Table.

Result

Two types T_1 and T_2 are equivalent with respect to mating, if and only if their proportions of self-mating and their cross-mating preferences are identical, and if all types cross-mate with them in a conditionally random manner, i.e. if

$$(a)\ P_1^s = P_2^s; \quad (b)\ U^c_{i \lhd 1} = U^c_{i \lhd 2} \text{ for all } i; \quad (c)\ U^c_{1 \lhd i} = U^c_{2 \lhd i} \text{ for all } i.$$

It must not be overlooked that, whenever two types have equal proportions of self-mating under arbitrary but given cross-mating norms, mating equivalence can always be constructed by setting the cross-mating references equal to the cross-mating norms. Consequently, mating equivalence always depends on the choice of cross-mating references. The cross-mating reference is meaningless only in the presence of complete self-mating, i.e. when $P_1^s = P_2^s = 1$.

The formal relationship between the cross-mating norms and the mating norms can be easily derived with the help of the proportions of self-mating P_i^s. Since $1 - P_i^s$ is the proportion of all cross-matings among all matings performed by T_i-individuals, it holds that:

$$P^c_{j \lhd i} = \frac{P_{j \lhd i}}{1 - P_i^s} \text{ for } i \neq j, \text{ and } P^c_{i \lhd i} = \frac{P_{i \lhd i} - P_i^s}{1 - P_i^s}. \tag{1.4}$$

As is to be expected, in the absence of self-mating, as is the case, for example, in dioecious or completely consecutively cosexual populations, the cross-mating norm is equal to the mating norm. This is also true of the cross-mating references and the mating references, so that in this case the mating equivalence of two types T_1 and T_2 is tantamount to $U_{i \lhd 1} = U_{i \lhd 2}$ and $U_{1 \lhd i} = U_{2 \lhd i}$ for all i.

The applicability of the term "mating equivalence" is broad and plays an important role particularly in population genetics. For example, different genotypes can produce the same phenotype when one allele is completely dominant over another. The question as to whether the various genotypes in a population which produce a single type are actually equivalent in mating can be of decisive importance for the establishment or maintenance of this type in the population. By way of pleiotropic gene effects, it is possible that these genotypes, which show no variation for the trait under study, give rise to different expressions with respect to another trait.

Consequences for the mating frequencies: The conditions for mating equivalence formulated above in terms of mating preferences will now be translated into conditions in terms of mating frequencies. In connection with conditions (a), (b) and (c), equation (1.4) yields:

$$\begin{aligned}(P_{i\lhd 1} - \delta_{i1}P_1^s)\cdot R^c_{i\lhd 2} &= (P_{i\lhd 2} - \delta_{i2}P_2^s)\cdot R^c_{i\lhd 1} \quad \text{and}\\ (P_{1\lhd i} - \delta_{i1}P_1^s)\cdot R^c_{2\lhd i} &= (P_{2\lhd i} - \delta_{i2}P_2^s)\cdot R^c_{1\lhd i}\ .\end{aligned} \tag{1.5}$$

Since individuals of the types T_1 and T_2 are taken to be completely equivalent, they can be subsumed under a single type T_0, so that then $P(T_0) = P(T_1)+P(T_2)$, $P(T_0\times T_0) = P(T_1\times T_1)+P(T_1\times T_2)+P(T_2\times T_2)$, $P(T_0 \times T_i) = P(T_1 \times T_i) + P(T_2 \times T_i)$ for $i \geq 3$ and $P_0^s = P_1^s = P_2^s$ hold. In this respect, it is important to ask in what way the matings of all T_0-individuals already determine the matings of the constituent types T_1 and T_2.

For $i \geq 3$, it follows immediately from equation (1.5) that:

$$P_{0\lhd i} = P_{1\lhd i} + P_{2\lhd i} = P_{1\lhd i}\left(1 + \frac{R^c_{2\lhd i}}{R^c_{1\lhd i}}\right) = P_{2\lhd i}\left(1 + \frac{R^c_{1\lhd i}}{R^c_{2\lhd i}}\right)$$

and hence

$$\begin{aligned}P(T_1 \times T_i) &= P(T_0 \times T_i)\cdot\frac{R^c_{1\lhd i}}{R^c_{0\lhd i}}\ ,\\ P(T_2 \times T_i) &= P(T_0 \times T_i)\cdot\frac{R^c_{2\lhd i}}{R^c_{0\lhd i}}\ ,\end{aligned} \tag{1.6a}$$

where $R^c_{0\lhd i} = R^c_{1\lhd i} + R^c_{2\lhd i}$. Setting $i = 1$ and $i = 2$ in the second of the two equations (1.5) and multiplying by $P(T_1)$ and $P(T_2)$, respectively, one obtains

$$\begin{aligned}P(T_1 \times T_1) &= P_0^s \cdot P(T_1) + \frac{1}{2}P(T_1 \times T_2)\cdot\frac{R^c_{1\lhd 1}}{R^c_{2\lhd 1}}\ ,\\ P(T_2 \times T_2) &= P_0^s \cdot P(T_2) + \frac{1}{2}P(T_1 \times T_2)\cdot\frac{R^c_{2\lhd 2}}{R^c_{1\lhd 2}}\ .\end{aligned} \tag{1.6b}$$

This in turn yields

$$\begin{aligned}P(T_0 \times T_0) &= P(T_1 \times T_1) + P(T_1 \times T_2) + P(T_2 \times T_2)\\ &= P_0^s \cdot P(T_0) + P(T_1 \times T_2)\cdot\left[1 + \frac{1}{2}\left(\frac{R^c_{1\lhd 1}}{R^c_{2\lhd 1}} + \frac{R^c_{2\lhd 2}}{R^c_{1\lhd 2}}\right)\right]\ ,\end{aligned}$$

and thus

$$P(T_1 \times T_2) = \bigl[P(T_0 \times T_0) - P_0^s P(T_0)\bigr] \cdot \frac{2R^c_{1\lhd 2}R^c_{2\lhd 1}}{R^c_{1\lhd 1}R^c_{1\lhd 2} + 2R^c_{1\lhd 2}R^c_{2\lhd 1} + R^c_{2\lhd 2}R^c_{2\lhd 1}} \tag{1.6c}$$

Setting $i = 1$ in both equations (1.5), it is evident that $R^c_{1\lhd 2}/R^c_{2\lhd 1} = P_{1\lhd 2}/P_{2\lhd 1} = P(T_1)/P(T_2)$ holds, and therefore

$$\begin{aligned} P(T_1) &= P(T_0) \cdot \frac{R^c_{1\lhd 2}}{R^c_{1\lhd 2} + R^c_{2\lhd 1}} \ , \\ P(T_2) &= P(T_0) \cdot \frac{R^c_{2\lhd 1}}{R^c_{1\lhd 2} + R^c_{2\lhd 1}} \end{aligned} \tag{1.6d}$$

results.

Equations (1.6) answer the question as to the form of the relations between the mating frequencies of T_0-individuals taken altogether and those of the two types T_1 and T_2, of which T_0 is composed. However, it has to be taken into account that the equations (1.6*b*) through (1.6*d*) have no meaning if, for example, T_1 and T_2 are female types, since in this case, the pertinent mating frequencies are all equal to 0. Here only the equations (1.6*a*) are applicable, and from these equations the values for $P(T_1)$ and $P(T_2)$ can also be derived by summation over i.

1.6 Application to an experimental data set

The above-developed methods for the representation and characterization of mating systems will now be briefly illustrated with the help of the experimental results that were obtained by Majerus et al. for a population of *Adalia bipunctata*.

In this population three types were distinguished which will be denoted by type 1, 2, and 3. Type 1 comprises two forms, *quadrimaculata* and *sexpustulata*, the types 2 and 3 refer to the forms *typica* and *annulata*, respectively. All three types appear in both sexes of this dioecious population, so that, taking account of the sex (F= female, M= male), six different types have to be distinguished: the female types T_{F1}, T_{F2}, T_{F3}, and the male types T_{M1}, T_{M2}, T_{M3}. The relative frequencies of these

Table 1

Circumstances of mating in a population of
Adalia bipunctata

* *

Mating frequencies and frequencies of types

		♀				
	Type	1	2	3	$P(T_{Mi})$	Q_i^M
	1	.148	.219	.095	.231	.318
♂	2	.130	.166	.047	.172	.458
	3	.071	.053	.071	.097	.224
	$P(T_{Fi})$	.175	.219	.106		
	Q_i^F	.308	.485	.207		

Mating preferences and mating success

Male preferences ($U_{Fi \triangleleft Mj}$)

		♂			
	Type	1	2	3	h_{Fi}
	1	1.040	1.227	1.188	1.136
♀	2	0.977	0.995	0.563	0.903
	3	0.993	0.660	1.768	1.024

Female preferences ($U_{Mj \triangleleft Fi}$)

		♀			
	Type	1	2	3	h_{Mi}
	1	1.330	1.572	1.409	1.453
♂	2	0.811	0.828	0.484	0.751
	3	0.906	0.540	1.495	0.866

types in the population will be denoted by Q_{Fi} and Q_{Mi} $(i = 1, 2, 3)$. Hence, $\sum_i (Q_{Fi} + Q_{Mi}) = 1$, and $Q_F := \sum_i Q_{Fi}$ and $Q_M := \sum_i Q_{Mi}$ are the proportions of female and male individuals in the population. From this the relative frequencies of the types within each of the sexes are $Q_i^F := Q_{Fi}/Q_F$ and $Q_i^M := Q_{Mi}/Q_M$. For $i, j = 1, 2, 3$, the “natural” mating references are therefore given by $R_{Mi \lhd Fj} = Q_i^M$ and $R_{Fj \lhd Mi} = Q_j^F$.

With dioecious populations the number of matings performed in each of the sexes must be the same, i.e. $P(T_F) = P(T_M) = \frac{1}{2}$, where $P(T_F) = \sum_i P(T_{Fi})$ and $P(T_M) = \sum_i P(T_{Mi})$. In general, this does not, of course, carry over to the sex ratio in the population, so that Q_F and Q_M need not always be identical. However, for an evaluation of the mating success, i.e. $h_{Fi} = P(T_{Fi})/Q_{Fi}$ and $h_{Mi} = P(T_{Mi})/Q_{Mi}$ it is in most cases sufficient to assume a 1:1 sex ratio $(Q_F = Q_M = \frac{1}{2})$, so that one obtains $h_{Fi} = 2 \cdot P(T_{Fi})/Q_i^F$ and $h_{Mi} = 2 \cdot P(T_{Mi})/Q_i^M$. Table 1 summarizes the mating frequencies $P(T_{Fi} \times T_{Mj})$, the frequencies Q_i^F, Q_i^M of the types in the population (as given by Majerus et al.), and the resulting female $(U_{Mi \lhd Fj})$ and male $(U_{Fi \lhd Mj})$ mating preferences as well as the mating successes.

A direct comparison of the mating frequencies with the relative frequencies of the single types in the population $(Q_i^M$, Q_i^F, see upper part of Table 1) does not reveal simple rules or laws characterizing the mating process. For example, the most frequent type among the females as well as among the males is type 2. However, among the matings the mating type $T_{F2} \times T_{M2}$ is only the second most frequent. A similar statement applies to the least frequent type 3. As compared to this, consideration of the mating preferences provides more specific insight.

The single male types differ from each other markedly in their preference patterns for the female types (see lower left part of Table 1). In essence, males of type 1 mate at random with all female types, since their U-values are all very close to 1. This is not true for the other two male types, among which type 2 shows no preferences for females of the same type, and its marked negative preference for females of type 3 is to some degree balanced by a less marked positive preference for females of type 1. On the other hand, males of type 3 show a strong positive preference for females of their own type and are thus in opposition to males of type 2, which show a strong negative preference for females of type 3. These opposite tendencies have as a consequence the leveling of female mating successes (the h_{Fi}’s are all very close to 1).

The mating preferences of the females (lower right part of Table 1) also show different but not necessarily opposite tendencies. Here, primarily males of type 1 are preferred, which, in the last analysis, results in a remarkable superiority of this type over all other male types in mating success. More advanced and elaborate characterizations of the mating system represented by these data and its effects on mating success require more detailed studies of special classes of mating systems, as will be introduced in the following sections.

2. Classification of mating systems

The previous considerations have shown that mating systems can be characterized directly via the comparison between mating norms and mating references with the help of mating preferences. It turned out that the most elementary characterization consists in the observation of the presence or absence of mating preferences and thus of random mating. This observation depends on the choice of the mating reference, which is basically limited by the compatibility relationships between the sexual types. The simplest mating reference, which is also the most important for purposes of classification of mating systems, therefore considers only the compatibility relationships between the sexual types. As a consequence, the so-called **natural mating reference** was introduced in order to characterize the situation where all types of the same sex have the same mating reference. The following classification into systems of random mating and certain systems deviating from this will be built on such natural references.

2.1 Random mating in cosexual populations

In genuinely cosexual populations only one sexual type exists, so that (according to the assumption of natural mating references) all types have the same mating reference, i.e. $R_{j\lhd i}$ does not depend on i. Thus $R_{j\lhd i} = R_j$ for all mating types, and $\sum_j R_j = 1$. Random mating refers to the absence of mating preferences and is formally represented by $U_{j\lhd i} = 1$. It follows therefore from equation (1.1): $\frac{1}{2}(1+\delta_{ij}) \cdot P(T_i \times T_j) = R_j \cdot P(T_i)$. In the case where all types mate at random, summation of the last equation over i yields $P(T_j) = R_j$ for all j. Since $[\frac{1}{2}(1+\delta_{ij})]^{-1} = 2 - \delta_{ij}$, one arrives at the result stated in the following Table.

Result

For a cosexual population in which all types mate at random with respect to natural mating references, it holds that for all types T_i and T_j

$$P(T_i \times T_j) = (2 - \delta_{ij}) \cdot P(T_i) \cdot P(T_j). \tag{2.1}$$

Consequently, in this case the mating frequencies are already completely determined by the frequencies with which the single types participate in all matings performed in the population. Since these frequencies enter the above equation as products, the mating frequencies will be said to have a **product structure**. It must be emphasized, however, that in cosexual populations in which random mating is observed for other than natural mating references, the mating frequencies will generally not show a product structure.

The existence of a product structure can also be inferred solely from certain relationships between the mating frequencies, i.e. without having to compute the mating participations $P(T_i)$. If a product structure is given in the above form, then it follows easily that the relationship $P(T_i \times T_j)^2 = 4P(T_i \times T_i)P(T_j \times T_j)$ holds for all $i \neq j$. In the reverse direction, if this relationship is realized and rewritten in the form $\frac{1}{2}P(T_i \times T_j) = \sqrt{P(T_i \times T_i)P(T_j \times T_j)}$, then summation over j, $j \neq i$ yields: $P(T_i) - P(T_i \times T_i) = \sqrt{P(T_i \times T_i)}\left[\sum_j \sqrt{P(T_j \times T_j)} - \sqrt{P(T_i \times T_i)}\right]$, and thus $P(T_i) = \sqrt{P(T_i \times T_i)}\sum_j \sqrt{P(T_j \times T_j)}$. Moreover, since $\sum_i P(T_i) = 1$, the identity $\sum_i \sqrt{P(T_i \times T_i)} = 1$ must hold. One thus obtains $P(T_i \times T_i) = P(T_i)^2$, and from this $P(T_i \times T_j) = 2P(T_i)P(T_j)$ for $i \neq j$. Hence the result in the following Table.

Result

In cosexual populations the mating frequencies possess a product structure if and only if

$$P(T_i \times T_j)^2 = 4 \cdot P(T_i \times T_i) \cdot P(T_j \times T_j) \tag{2.2}$$

holds for all $i \neq j$.

Choosing the mating reference in accordance with the relative frequencies Q_i of T_i-individuals in the population, it follows that $R_i = Q_i$ and thus $h_i = 1$ for all types. Hence, with natural mating references, random mating in cosexual populations excludes the possibility of differential mating success of the single types. In this sense random mating is non-selective.

Even for natural mating references the observation of mating frequencies showing a product structure does not per se allow the conclusion that the population mates randomly. However, under the assumption of natural mating references, the observation of a product structure has another interesting and generally valid consequence for the structure of mating preferences. It turns out that in this case $U_{j \lhd i} = P(T_j)/R_j$, and that therefore $U_{j \lhd i}$ is independent of i. In other words, *if, under the assumption of natural mating references in a cosexual population, the mating frequencies show a product structure, then all types must display the same pattern of mating preferences.* Consequently, if the mating reference is identical to the frequency distribution of the types in the population, the mating success of each type is identical to the degree to which it is preferrred ($h_j = U_{j \lhd i}$).

2.2 Random mating in dioecious populations

The assumption of natural mating references in both sexes implies that within either sex all types have the same mating reference. It thus holds that $R_{Mj \lhd Fi} = R_{Mj}$ with $\sum_j R_{Mj} = 1$, and $R_{Fi \lhd Mj} = R_{Fi}$ with $\sum_i R_{Fi} = 1$.

For the time being, let us assume that in only one sex, the male sex, say, all types mate at random, i.e. $U_{Fi \lhd Mj} = \frac{1}{2} P(T_{Fi} \times T_{Mj})/[R_{Fi} \cdot P(T_{Mj})] = 1$ for all i and j. Hence, $\frac{1}{2} P(T_{Fi} \times T_{Mj}) = R_{Fi} \cdot P(T_{Mj})$, and summation of this equation over j yields $P(T_{Fi}) = \frac{1}{2} R_{Fi}$. Here the relationship $\sum_j P(T_{Mj}) = P(T_M) = \frac{1}{2}$ was used again. Similarly to the result for cosexuality, one again obtains a product structure for the mating frequencies, however, it is now of the form $P(T_{Fi} \times T_{Mj}) = 4 \cdot P(T_{Fi}) \cdot P(T_{Mj})$. In an analogous manner one arrives at exactly the same result for random mating of all female types ($U_{Mj \lhd Fi} = 1$ for all i and j). The result is summarized in the following Table.

Result

For natural mating references in both sexes of a dioecious population, random mating of at least one sex implies a product structure for the mating frequencies, i.e.

$$P(T_{Fi} \times T_{Mj}) = 4 \cdot P(T_{Fi}) \cdot P(T_{Mj}). \tag{2.3}$$

Even though random mating of the male or female sex has the same consequence for the mating frequencies, it would be incorrect to infer from this that random mating of one sex automatically enforces random mating of the other. In the same manner, as was already true for cosexuality, it would be incorrect to infer random mating of either sex from the existence of a product structure.

As was pointed out earlier, studies of the effects of random mating on mating success requires us to choose the natural mating reference in accordance with the relative frequencies Q_{Fi} and Q_{Mj} of the female types T_{Fi} and the male types T_{Mj} in the population, respectively. As was mentioned in connection with the analysis of the data on *Adalia bipunctata*, the quantities $Q_F := \sum_i Q_{Fi}$ and $Q_M := \sum_j Q_{Mj}$ are the proportions of all female and male individuals, respectively, in the population, while $Q_i^F := Q_{Fi}/Q_F$ and $Q_j^M := Q_{Mj}/Q_M$ are the relative frequencies of the types within the respective sex. However, in contrast to this data analysis, it will now be allowed that $Q_F \neq Q_M$. The mating reference is then given by $R_{Fi} = Q_i^F$ for the males and by $R_{Mj} = Q_j^M$ for the females.

Considering, as before, random mating for the male sex, the mating preferences of this sex can be computed with the help of (2.3):

$$1 = U_{Fi \triangleleft Mj} = \frac{2P(T_{Fi})}{R_{Fi}} = 2Q_F \cdot \frac{P(T_{Fi})}{Q_{Fi}}.$$

In this expression $P(T_{Fi})/Q_{Fi} = h_{Fi}$, and therefore $h_{Fi} = (2Q_F)^{-1}$. Thus, all female types have the same mating success.

However, with respect to the mating preferences of the female sex one obtains

$$U_{Mj \triangleleft Fi} = \frac{2Q_M P(T_{Mj})}{Q_{Mj}} = 2Q_M \cdot h_{Mj},$$

so that all female types show the same pattern of mating preferences, and the mating successes of the male types are proportional to their preference by the females. This proportionality becomes an identity if the sex ratio is 1:1, i.e. if $Q_M = Q_F = \frac{1}{2}$. Random mating of the female sex yields an analogous result. Hence the result stated in the following Table.

Result

If the natural mating references are in accordance with the frequencies of the types in a dioecious population, then random mating of one sex implies that all types of the other sex have the same pattern of mating preferences and identical mating success. The mating successes of the types in the random mating sex are equal to their preferences by the other sex.

This result once more illustrates the previous finding that random mating may be realized in one but not in the other sex. Yet, random mating of one sex puts restrictions on the mating behaviour of the other in that the types in the latter sex cannot differ in their patterns of mating preferences.

Finally, it shall be pointed out once more that the notion of dioecy is usually referred to individuals in the diplophase. In a generalized form, however, the term can also be applied to the haplophase when the gametes are addressed with respect to both types of sexual specificity. The above findings can therefore be transferred to cosexual organisms by assigning each individual two sexual functions via their male and female gametes, and by defining the mating event as the fusion of a male with a female gamete.

2.3 Sexual selection

In order to explain the evolution of secondary sex traits in dioecious animals, Darwin (1859, p.88) introduced the notion of "sexual selection", and he originally defined it as the competition or struggle in one sex, primarily the male sex, for the possession of the other sex. The more successfully a type survives this struggle, the greater are its chances to participate in the mating process, provided the other sex accepts the "winner" without discrimination. The principle of sexual selection consists in the conception that in one sex forces are active that imply differential mating success within this (the selected) but not within the other sex, and that the types of the non-selected sex have no differential mating preferences. With the help of the results in the last section, it will now be demonstrated that sexual selection, in this sense, is tantamount to a very particular system of mating.

Suppose that the sexually selected sex is the male sex. Then all female types have the same mating success, i.e. $h_{Fi} = h_F$ for all i, and the same mating preferences, i.e. $U_{Mj\triangleleft Fi} = U_{Mj}$ for all i and j. Under the assumption of natural mating references which are chosen in accordance with the frequencies of the types in the population, it follows from $U_{Mj\triangleleft Fi} = U_{Mj}$ that $\frac{1}{2}P(T_{Fi} \times T_{Mj}) = U_{Mj}Q_j^M P(T_{Fi})$. Summation of this equation over i yields $P(T_{Mj}) = \frac{1}{2}U_{Mj}Q_j^M$, so that the mating frequencies have a product structure. Furthermore, from $h_{Fi} \equiv h_F$ it follows that $P(T_{Fi}) = h_F Q_{Fi}$, which, after summation over i, leads to $h_F Q_F = \frac{1}{2}$. Hence, $P(T_{Fi}) = \frac{1}{2} Q_i^F$. Combining these two results, one obtains

$$U_{Fi \triangleleft Mj} = \frac{2 \cdot P(T_{Fi}) \cdot P(T_{Mj})}{Q_i^F \cdot P(T_{Mj})} = 1,$$

and thus random mating of the male sex.

On the other hand, assuming random mating for the male sex, the results of the previous section tell us that all types of the female sex have the same pattern of mating preferences, which, in turn, means sexual selection for the male sex. Again, the role played by the sexes can be reversed, and one thus arrives at the finding stated in the following Table.

Result

Sexual selection, *in the original Darwinian sense, is tantamount to random mating of all types in one sex of a dioecious population, where the natural mating references are chosen in accordance with the frequencies of the types in this population. The random mating sex is the sexually selected sex.*

This formulation gives prominence to the fact that sexual selection may also arise if only one but not the other sex shows mating preferences. The sex showing the preferences then determines the mating successes of the types in the other sex which has no preferences. In connection with the remarks at the end of the last section it becomes furthermore evident that the notion of sexual selection is not only restricted to dioecious populations but can also be applied to cosexual organisms by distinguishing for each individual its two gametic sex functions. The classification as a particular system of mating is therefore also a useful tool for the detection of sexual selection in less obvious situations.

When viewed in an evolutionary context, sexual selection for a particular trait is frequently conceived of as evolutionary changes in this trait that take place in one sex only, i.e. independently of and not affecting the other sex. This concept of evolutionary independence appears particularly appropriate when applied to sex specific traits. However, the fact that a trait is expressed in only one sex is by itself not yet sufficient to classify it as sexually selectable in the sense of evolutionary independence. For example, if the gene loci participating in the control of the variation of this trait act pleiotropically on another trait which is expressed (not necessarily only) in the other sex, then, when referred to these two traits, the circumstances of mating may not be in accordance with the above characterization of sexual selection.

Even more so, the question arises as to whether independent evolution of the selected sex can be realized if the same trait expressions occur in both sexes and are controlled by the same genes. It is easily conceivable that in one sex the mating behavior does not depend on the trait expressions concerned, while this need not be simultaneously true for the other sex. However, this does again not exclude the possibility that the frequencies of the genotypes involved change in both sexes, and that this carries over to the frequencies of the trait expressions in both sexes. In such a case the evolution of the sexes would be correlated. For autosomal gene loci this can even be expected to be the rule rather than the exception, so that the above evolutionary concept of sexual selection is in this case very unlikely to be realized in its strict sense.

Sexual selection in the sense of independent evolution of one sex is therefore primarily restricted to traits, the variation of which is controlled in the two sexes by different, non-pleiotropically acting, and non-linked gene loci. These considerations do of course not affect the present general characterization of sexual selection as a system of mating, and this characterization should in any case be given priority in order to avoid confusion of causes with effects and vice versa.

2.4 Classification of mating systems by product structures

In the course of the above analyses, some systems of mating have been treated which imply product structures for their mating frequencies. Thus the question arises as to whether certain classes of systems of mating can be inferred solely from the observation of mating frequencies showing a product structure. This question gains relevance in all situations (which are by no means exceptional) where individuals can be identified only during or after (in the result of) the mating process, so that no further information about pre-mating references is available.

An answer is provided by the previously obtained result that for natural mating references in cosexual populations a product structure for the mating frequencies implies that all types have the same pattern of mating preferences (see end of section 2.1). Conversely, if all types have the same pattern of mating preferences, i.e. $U_{i\lhd j} = U_i$ for all i and j, one obtains $\frac{1}{2}(1+\delta_{ij}) \cdot P(T_i \times T_j) = U_i \cdot P(T_j) \cdot R_i$ and, after summation over j, $P(T_i) = U_i \cdot R_i$. Consequently, $\frac{1}{2}(1+\delta_{ij})P(T_i \times T_j) = P(T_i) \cdot P(T_j)$, so that the mating frequencies necessarily display a product structure.

Result

In a cosexual population where the system of mating is based on natural mating references, the mating frequencies show a product structure if and only if all types have the same pattern of mating preferences.

An analogous result can be derived for dioecious populations under the even less restrictive assumption that only one of the two sexes, the male, say, is referred to natural mating references ($R_{Fi\lhd Mj} = R_{Fi}$). Given a product structure, it indeed follows that $U_{Fi\lhd Mj} = 2 \cdot P(T_{Fi})/R_{Fi}$, so that all male types have the same mating preferences. On the other hand, if $U_{Fi\lhd Mj} = U_{Fi}$ is given, one obtains $\frac{1}{2}P(T_{Fi} \times T_{Mj}) = U_{Fi} \cdot P(T_{Mj}) \cdot R_{Fi}$ and from this, after summation over j, $P(T_{Fi}) = \frac{1}{2}U_{Fi} \cdot R_{Fi}$, which again yields a product structure for the mating frequencies. Here, the roles of the sexes are of course exchangeable.

Result

The mating frequencies in a dioecious population, in which one sex is assigned natural mating references, display a product structure if and only if all types in this sex have the same pattern of mating preferences.

If both sexes are assigned natural mating references, and if the mating frequencies show a product structure, then in each of the sexes all types have the same pattern of mating preferences. This answers the initially posed question for cosexual as well as for dioecious populations completely: Even though, in both systems of sexuality, product structures cannot be accepted as an indicator of random mating, they nevertheless uniquely characterize a very specific class of mating systems. When referred to natural mating references, this class excludes all systems of mating in which different types of the same sex also differ in their patterns of mating preferences.

2.5 Assortative mating

As is suggested by the term “assortative” itself, here systems of mating are addressed that differ from random mating. The classical forms of assortative mating are positive and negative assortative mating, which were introduced in section 1.2 in connection with mating preferences. These terms can be meaningfully applied only to those traits for which similarities or dissimilarities between potential mating partners are definable. This is the case, for example, if in both sexes of a dioecious population the same trait variable (such as weight of individuals or their genotypes at an autosomal locus) is considered. In cosexual populations with natural mating references, such similarity relationships are automatically defined for each trait, simply because each type has itself as a potential mating partner.

Although positive and negative assortative mating are usually based on phenotypic or genetic traits, all suitable traits can, at least in principle, be considered. This includes, for example, traits used in studies of migration. In order to investigate the dependence of mating on the spatial distribution of the members of a population, a typification according to the location of origin of an individual is advisable. Preferential mating among neighbouring individuals can then be regarded as a form of positive assortative mating. In the same manner, genealogical traits can be used for studies of mating among relatives. Here, the typification takes place according to aspects of common ancestry, i.e., all individuals which descend from certain given common ancestors are subsumed under a single type. Such genealogically defined types are often termed “families”, such as full sib families, half sib families, etc.. Preferential mating between individuals of the same or similar genealogical types is called **inbreeding**, and thus inbreeding is tantamount to genealogically positive assortative mating. To this category of systems of mating belongs individual self-mating, which is well known as complete or partial self-fertilization in cosexual (hermaphroditic or monoecious) plant populations.

Positive and negative assortative mating thus differ from the class of mating systems treated in the previous section in that the matings are preferential, but, at least for two types of the same sex, the patterns of preferences are not identical. The latter lays the basis for a generalized definition of the term “assortative mating”, which also includes systems that cannot be classified as positive or negative assortative mating:

Definition

Assortative mating *is realized if at least two different types with equal mating references differ with respect to their patterns of mating preferences. This is the case in cosexual or dioecious populations with natural mating references, if and only if the mating frequencies do not exhibit a product structure.*

The statement in the second sentence follows immediately from the results of the preceding section, and, as was emphasized there, it has the important consequence that assortative mating can already be recognized from experimental data that provide knowledge about mating frequencies but not about the frequencies of the types in the population. However, in most cases the mating preferences give a clearer impression about the existence of assortative mating. The experimental results for a population of *Adalia bipunctata* listed in Table 1 will again serve as a demonstration. It suffices to consider the mating preferences of only one of the two sexes in order to find that assortative mating is realized here. Assortative mating is even very pronounced, since in none of the sexes can even two types be found showing sufficiently similar patterns of mating preferences. As opposed to this, no such clear statement can be derived from a comparison of the mating frequencies with their corresponding product structure: in no case do the absolute differences $|P(T_{Fi} \times T_{Mj}) - 4P(T_{Fi})P(T_{Mj})|$ exceed a value of 0.032. On the basis of such a comparison (which is almost standard in studies of this kind), one would rather have been inclined to rate the amount of assortative mating as minor without having performed a very detailed statistical analysis.

2.6 Random preferential mating

In many cases a comparison of two types with respect to their patterns of mating preferences is meaningful only if they are identical in their mating references. This also explains the prominence frequently given (consciously or unconsciously) to natural mating references for the characterization of mating systems. Applying this principle of comparability to the characterization of all non-assortative systems of mating, one arrives at a representation that reveals a certain resemblance to random mating, and which furthermore includes sexual selection and systems characterized by product structures as special cases.

Random mating is specified by the fact that a type shows no differential mating preferences for its potential mating partners. Hence, in this concern equality of the preferences *within* a type is addressed. Under the assumption of equal mating references this is opposed by equality of preferences *between* two or more types. This situation was referred to as "random preferential mating" by O'Donald (1980 p.21) and it leads us to the following formal definition:

Definition

Random preferential mating *is realized in a population if all types having identical mating references also have identical patterns of mating preferences.*

Random preferential mating must not be confounded with mating equivalence (see section 1.5). Only if individual self-mating does not occur and if all types with identical mating references are mating-equivalent, do matings occur randomly preferentially. Furthermore, one recognizes immediately for cosexual or dioecious populations based on natural mating references that randomly preferential mating is equivalent to the existence of product structures. Hence, the notion of sexual selection in the Darwinian sense (see section 2.3) is a special case of random preferential mating, where the mating preferences of one sex (but not the other) are all identical to 1. Some authors (see e.g. Christiansen 1977) apply the notion of sexual selection also to randomly preferential mating populations in which none of the two sexes mates at random. However, this seems to contradict the original concept of Darwin, since in this concept it is the sexually selected sex which must mate at random.

Given natural mating references for one sex of a dioecious population, then an investigation of the mating preferences of only one sex already suffices for the detection of random preferential mating. For example, given natural mating references $R_{Fi \triangleleft Mj} = R_{Fi}$ for the male sex, then, according to section 2.4, the mating frequencies display a product structure if all types of the male sex have the same pattern ($U_{Fi \triangleleft Mj} = U_{Fi}$) of mating preferences. Consequently, $U_{Mj \triangleleft Fi} = 2P(T_{Mj})/R_{Mj \triangleleft Fi}$, and all female types with equal mating references have equal patterns of mating preferences. With the help of this result the additional insights into characteristics of assortative mating stated in the following Table are easily derived.

Result

If natural mating references are given for one sex of a dioecious population, and if all types of this sex have the same pattern of mating preferences, then the whole population mates randomly preferentially. Hence, assortative mating can already be excluded if in only one sex all types have the same pattern of mating preferences and if this sex is assigned natural mating references.

3. Models of random mating

3.1 Cosexuality: Effects of random mating in the haplophase on the mating frequencies in the diplophase

Cosexuality is characterized by the capacity of an individual to produce male as well as female gametes. The notion of the individual refers here to the diplophase, and the typification by trait expressions is also oriented at this phase. The gametes can, in turn, themselves be conceived of as individuals belonging to the haplophase, so that, on this level, a system of sexuality exists which is equivalent to that of dioecy. Denoting by T_i the type of an individual in the diplophase, it therefore suggests itself to assign to each gamete in addition to its sex the type of its producer. The gametes of an individual (in the diplophase) of type T_i are then typified by T_{Fi} in case they are female and T_{Mi} in case they are male. The additional symbols M and F appearing in the subscript thus characterize individuals of the haplophase, whereas in the absence of these symbols individuals of the diplophase are referred to. The quantities defined in the following Table of notations are built upon this stipulation.

Notations

$Q_i :=$ relative frequency of T_i-individuals (in the diplophase);

$f_i, m_i :=$ average number of female and male gametes, respectively, produced by a T_i-individual (female and male **fertilities**, respectively);

$\bar{f} := \sum_i Q_i \cdot f_i$, or average number of female gametes produced by an individual of the diplophase (in the total population; average female fertility);

$\bar{m} := \sum_i Q_i \cdot m_i$, or average number of male gametes produced by an individual of the diplophase (in the total population; average male fertility);

$Q_i^F := Q_i \cdot f_i / \bar{f} =$, or relative frequency of T_{Fi}-gametes among all female gametes;

$Q_i^M := Q_i \cdot m_i / \bar{m} =$, or relative frequency of T_{Mi}-gametes among all male gametes.

In order to be able to solve the above-posed problem, it must first be made clear what has to be conceived of as mating in the diplophase and in the haplophase. As was preliminarily mentioned, a mating event in the haplophase is simply defined as the fusion of two gametes and thus as the formation of a zygote. When transferred to the diplophase, the definition of a mating event remains the same, however, with the difference that the fusing gametes are now considered as representing their diploid producers. Hence, if two individuals of the diplophase produce several zygotes, then the number of such zygotes is set equal to the number of matings performed by the pair of individuals.

It will now be assumed that, on the basis of natural mating references, random mating is realized among all types of the haplophase (random fusion of the gametic types). The mating references for the female gametic types are given by the relative frequencies Q_i^M among all male gametes produced, and in the same manner the Q_i^F's form the mating references for the male gametic types. One thus obtains for the mating references in the haplophase

$$R_{Mj \triangleleft Fi} = Q_j^M \quad \text{and} \quad R_{Fi \triangleleft Mj} = Q_i^F .$$

According to equation (1.1) random mating in the haplophase, i.e. $U_{Mj \triangleleft Fi} = U_{Fi \triangleleft Mj} = 1$ (for all i, j), therefore implies $\frac{1}{2} P(T_{Mj} \times T_{Fi}) = P(T_{Fi}) \cdot Q_j^M = P(T_{Mj}) \cdot Q_i^F$ and thus

$$P(T_{Mj}) = \frac{1}{2} Q_j^M = \frac{1}{2} \frac{Q_j \cdot m_j}{\bar{m}}, \quad P(T_{F_i}) = \frac{1}{2} Q_i^F = \frac{1}{2} \frac{Q_i \cdot f_i}{\bar{f}}, \tag{3.1a}$$

$$P(T_{Mj} \times T_{Fi}) = 4 \cdot P(T_{Mj}) \cdot P(T_{Fi}) = \frac{Q_i \cdot Q_j \cdot f_i \cdot m_j}{\bar{f} \cdot \bar{m}}. \tag{3.1b}$$

Applying the above stipulation on mating in the diplophase, one obtains the mating frequencies in this phase from

$$\begin{aligned} &P(T_i \times T_j) = P(T_{Fi} \times T_{Mj}) + P(T_{Fj} \times T_{Mi}) \text{ for } i \neq j, \text{ and} \\ &P(T_i \times T_i) = P(T_{Fi} \times T_{Mi}); \\ &\qquad P(T_i) = P(T_{Fi}) + P(T_{Mi}). \end{aligned} \tag{3.2}$$

For the (cosexual) diplophase again natural mating references will be considered which are based on the frequencies of the diplo-types in the total population. Hence, $R_{i\lhd j} = Q_i$, and the *mating preferences in the diplophase* are therefore:

$$U_{i\lhd j} = \frac{\frac{1}{2}(1+\delta_{ij})P(T_i \times T_j)}{P(T_j)Q_i} = \frac{f_i m_j + f_j m_i}{f_j \bar{m} + m_j \bar{f}} \quad \text{for all } i \text{ and } j.$$

Even though it is not surprising that these mating preferences are frequency dependent, it is worth noting that, *for a given type, the ratios of its preferences for its potential mating partners are frequency independent*, i.e. $U_{i\lhd j}/U_{k\lhd j}$ is a constant with respect to frequencies.

Without application of particular assumptions on the fertilities, the mating preferences are not equal to 1. One thus can state: *Random mating in the haplophase does, in general, not imply random mating in the diplophase.* This raises the question as to which structures of the fertilities give rise to which classes of mating systems in the diplophase.

It can be demonstrated with the help of a simple proof* that random preferential mating, i.e. $U_{i\lhd j} = U_i$ for all i and j (see section 2.6), can exist only with **sexual symmetry** (when female and male fertilities are proportional, i.e. $f_i = c \cdot m_i$ for all i). From this the statements in the following Table on further classes of mating systems result immediately.

Result

Depending on the female and male fertilities, random mating in the haplophase can imply the following classes of mating systems in the diplophase:
▷ *random mating, if the types of the diplophase do not differ in their female nor in their male fertilities;*
▷ *random preferential mating, if the fertilities vary sexually symmetrically;*
▷ *assortative mating, if sexually asymmetrical fertilities exist.*

---

* Suppose that $U_{i\lhd j} = U_i$ for all i and j. Then $f_i m_j + f_j m_i = U_i(f_j \bar{m} + m_j \bar{f})$ and thus $f_j(m_i - U_i\bar{m}) = m_j(U_i\bar{f} - f_i)$. Assume that for at least one i $m_i \neq U_i\bar{m}$ holds; then $f_j = c \cdot m_j$ for all j, where $c = (U_i\bar{f} - f_i)/(m_i - U_i\bar{m})$. Inserting this into the above equation yields $2cm_im_j = 2U_icm_j\bar{m}$ and therefore $m_i = U_i\bar{m}$ for all i, which is a contradiction. In a similar manner one proves that the assumption $f_i \neq U_i\bar{f}$ is contradictory. Hence, $U_i = f_i/\bar{f} = m_i/\bar{m}$, i.e. the female fertilities f_i and male fertilities m_i are proportional.

Concerning *mating success* of the single types *in the diplophase*, i.e. $h_i = P(T_i)/Q_i$ for the type T_i, it is again easily seen that

$$h_i = \frac{1}{2}\left(\frac{f_i}{\bar{f}} + \frac{m_i}{\bar{m}}\right).$$

Consequently, the mating success of a type is equal to the arithmetic mean of its relative (with respect to the population average) female and male fertility.

3.2 Dioecy: The effect of random mating in the diplophase on the mating frequencies in the haplophase

In accordance with the last section, it will now again be assumed that the trait expressions (the typification) are determined for individuals of the diplophase, and that the gametes (haplophase) are characterized by the typification of their producers. As opposed to cosexuality, in dioecious populations the sex specificity of the gametes is identical with that of their producers, so that in the diplo- as well as in the haplophase female types are denoted by T_{Fi} and male types by T_{Mj}. A further difference lies in the fact that now the matings in the haplophase (fusion of a female with a male gamete) are to be viewed as the result of matings which are primarily defined for the diplophase. Thus the frequencies of matings among types of the haplophase are determined by the number of zygotes, which result from the single matings in the diplophase (see Kempthorne and Pollak 1970, or Roux 1977). The notations in the following Table reflect these facts.

Notations

Q_i^F, Q_j^M := relative frequency of T_{Fi}-individuals and T_{Mj}-individuals among all female and male individuals, respectively, in the diplophase.

$b_{i,j}$:= average number of zygotes which are produced in the diplophase by a mating of the type $T_{Fi} \times T_{Mj}$ (**fecundity** of this mating type).

b_{Fi}, b_{Mj} := average number of zygotes which are produced in the diplophase by a T_{Fi}- and a T_{Mj}-individual, respectively, among all such matings.

$\bar{b}$:= average number of zygotes produced per mating in the diplophase.

In order to be able to distinguish the mating frequencies in the diplophase from those in the haplophase, the superscripts D and H will be used, so that $P^D(...)$ and $P^H(...)$ refer to the mating frequencies in diplo- and haplophase, respectively.

Random mating of all types in the diplophase will again be based on natural mating references, i.e. the mating references in the diplophase are given by

$$R_{Fi\triangleleft Mj} = Q_i^F \text{ and } R_{Mj\triangleleft Fi} = Q_j^M \ .$$

For random mating of both sexes in the diplophase, this directly yields:

$$P^D(T_{Fi}) = \frac{1}{2}Q_i^F, \quad P^D(T_{Mj}) = \frac{1}{2}Q_j^M, \quad P^D(T_{Fi} \times T_{Mj}) = Q_i^F \cdot Q_j^M \ .$$

Since each mating of the type $T_{Fi} \times T_{Mj}$ in the diplophase produces on the average $b_{i,j}$ zygotes,

$$\begin{aligned} b_{Fi} &= \sum_j b_{i,j} \cdot P^D_{Mj\triangleleft Fi} = \sum_j b_{i,j} \cdot \frac{1}{2}P^D(T_{Fi} \times T_{Mj})/P^D(T_{Fi}) \\ &= \sum_j b_{i,j} \cdot Q_j^M, \end{aligned}$$

$$\begin{aligned} b_{Mj} &= \sum_i b_{i,j} \cdot P^D_{Fi\triangleleft Mj} = \sum_i b_{i,j} \cdot \frac{1}{2}P^D(T_{Fi} \times T_{Mj})/P^D(T_{Mj}) \\ &= \sum_i b_{i,j} \cdot Q_i^F, \\ \bar{b} &= \sum_{i,j} b_{i,j} \cdot P^D(T_{Fi} \times T_{Mj}) = \sum_{i,j} b_{i,j} \cdot Q_i^F \cdot Q_j^M \\ &= \sum_i b_{Fi} \cdot Q_i^F = \sum_j b_{Mj} \cdot Q_j^M \end{aligned}$$

hold. Hence, the relative frequencies of matings (fusions) of T_{Fi}- with T_{Mj}-gametes is equal to $P^D(T_{Fi} \times T_{Mj}) \cdot b_{i,j}/\bar{b}$, and the *mating frequencies in the haplophase* can be expressed as

$$P^H(T_{Fi} \times T_{Mj}) = Q_i^F \cdot Q_j^M \cdot b_{i,j}/\bar{b}, \tag{3.3a}$$

$$P^H(T_{Fi}) = \frac{1}{2}Q_i^F \cdot b_{Fi}/\bar{b}, \quad P^H(T_{Mj}) = \frac{1}{2}Q_j^M \cdot b_{Mj}/\bar{b}. \tag{3.3b}$$

This result can be interpreted as a special mating system for the individuals in the diplophase, if the original definition of mating is substituted by the fusion of two gametes, i.e. when the performance of a mating between two individuals of the diplophase is defined as the fusion of a gamete of the one individual with a gamete of the other. This corresponds to the notion of mating for cosexual populations used in the previous section. In this case the mating frequencies in the diplophase are identical to the above frequencies P^H in the haplophase. Maintaining the original mating references ($R_{Fi\triangleleft Mj} = Q_i^F$, $R_{Mj\triangleleft Fi} = Q_j^M$), one then obtains for the mating preferences:

$$U_{Fi\triangleleft Mj} = \frac{b_{i,j}}{b_{Mj}}, \quad U_{Mj\triangleleft Fi} = \frac{b_{i,j}}{b_{Fi}}.$$

These preferences account for the modification of the original system of random mating by differential fecundities of the mating types. It is remarkable that, as was the case in the previous model, again *the ratios of the mating preferences of a given type for its potential mating partners are frequency independent*, i.e. $U_{Fi\triangleleft Mj}/U_{Fk\triangleleft Mj}$ and $U_{Mj\triangleleft Fi}/U_{Mk\triangleleft Fi}$ are constants with respect to the frequencies.

Depending on the structure of the fecundities, several classes of mating systems can be realized that deviate from random mating. In detail, the classifications introduced in the last chapter allow to distinguish between the following systems of mating:

▷ *Random preferential mating:* According to the results of section 2.6, this system is realized in dioecious populations if and only if in at least one sex all types have the same pattern of mating preferences. As applied to the female sex, for example, this means that $U_{Mj\triangleleft Fi} = U_{Mj}$ for all i and j, which is in turn equivalent to $b_{i,j} = U_{Mj} \cdot b_{Fi}$. By multiplication of this equation with Q_i^F, subsequent summation over i yields $b_{Mj} = U_{Mj} \cdot \bar{b}$ and therefore $b_{i,j} = b_{Fi} \cdot b_{Mj}/\bar{b}$. Clearly, the same result is obtained if all types of the male sex are assumed to have the same pattern of mating preferences. Consequently, the product structure of the mating frequencies implied by random preferential mating is mirrored by a product structure of the fecundities.

▷ *Sexual selection:* This is a special case of random preferential mating in which the types of one sex (the sexually selected sex) mate at random. If this sex is the male, say, then $U_{Fi\triangleleft Mj} = 1$ must hold for all i and j, i.e. $b_{i,j} = b_{Mj}$. Hence, sexual selection of the male sex is equivalent to the situation where fecundity differences among the mating types are solely due to the male but not to the female types. The role of the sexes is, of course, exchangeable.

▷ *Assortative mating:* This system of mating is realized if the mating frequencies do not show a product structure (see section 2.5). According to the above demonstrations, this holds if and only if, for at least one mating type $T_{Fi} \times T_{Mj}$, its fecundity $b_{i,j}$ is not equal to $b_{Fi} \cdot b_{Mj}/\bar{b}$. The present model thus confirms in the special case the generally valid result derived in section 2.6, namely that assortative mating occurs either in both sexes simultaneously or never.

The main results can be summarized in the following Table.

Result

Consider a dioecious population in which all types of the diplophase mate at random with respect to the natural mating references, and in which the mating types are allowed to differ in their fecundities. If, under this supposition, mating events are newly defined by the fusion of gametes, then differential fecundities can lead to non-random mating. Hence, the fecundities of mating types can be conceived of as parameters of a mating system.

An alternative interpretation of the fecundities: The fact that fecundities can be conceived of as parameters of a mating system emphasizes once more the possibility that apparently intrinsically different components of the reproductive system may, in the last analysis, have identical effects on the mating system. The present model is particularly suited for a demonstration of this statement with the help of a concrete example.

As the first step, consider an extension of the definition of mating in the diplophase such that each contact between potential mating partners is already scored as a mating event. Based on this extended definition of mating, the assumption of random mating will be adhered to. As a second step, each contact will be assumed to have a certain probability u of "successful" mating between the partners involved; a contact is considered "successful" if it results in the production of zygotes. The mating probability u will depend on the respective mating type, so that $u_{i,j}$ denotes the fraction of successful matings among all contacts of the type $T_{Fi} \times T_{Mj}$ $(0 \leq u_{i,j} \leq 1)$. The average number of zygotes per successful mating will be assumed to be the same for all mating types (no fecundity differences at the level of successful matings) and will be denoted by b. Hence, the average number of zygotes produced per contact of the mating type $T_{Fi} \times T_{Mj}$ is equal to $u_{i,j} \cdot b$. Setting $u_{i,j} \cdot b = b_{i,j}$, one immediately recognizes the equivalence with the original fecundity model. Clearly, the difference between the two formulations lies solely in the definition of the mating event in the diplophase.

Yet, the formulation with the help of mating probabilities allows for two different interpretations of the previously computed mating preferences. The original computation was based on the definition of a mating event as the fusion of a pair of gametes. Since now all "successful" matings have identical fecundity, the representation of the mating preferences remains unchanged, provided their computation is based on just this "successful" mating as the unit of mating. Thus, the mating preferences U can be applied equally well to two definitions of mating, where one definition refers to the haplophase and the other to the diplophase.

3.3 Gynodioecy and androdioecy

These two systems of sexuality are characterized by the existence of two sexual types in the population, one cosexual and one unisexual type. Depending upon whether the unisexual sex is female or male, one speaks of gyno- or androdioecy, respectively. As was mentioned in the preliminary remarks, the unisexual sexes can, within these systems of sexuality, be conceived of as extreme cases of cosexuality in which only one of the two basically possible sex functions is realized. Consequently, the model introduced in section 3.1 can also be applied to treat these systems of sexuality; one simply has to regard that the number m_i of male gametes or f_i of female gametes of a type is zero if this type belongs to female or male sex, respectively. Hence, the results of section 3.1 carry over to the present systems of sexuality if mating is considered on the level of the gametes (haplophase), and if on this level random mating among all types is assumed. This situation will now be treated by the example of gynodioecy only, since corresponding results for androdioecy can be obtained simply by replacement of the female by the male sexual type.

In order to identify the sexual specificity of individuals in the diplophase, cosexual and female types will be denoted by T_{Bi} and T_{Fj}, respectively. The following definitions of symbols take account of this notation:

Notations

Q_{Bi}, Q_{Fj} := relative frequency of T_{Bi}- and T_{Fj}-individuals, respectively, in the diplophase. $Q_B := \sum_i Q_{Bi}$, $Q_F := \sum_j Q_{Fj}$ are the frequencies of cosexual and female individuals in the total population ($Q_B + Q_F = 1$).

f_{Bi}, m_{Bi} := average number of female and male gametes, respectively, of a T_{Bi}-individual.

f_j := average number of gametes (female) of a T_{Fj}-individual.

$\bar{f} := \sum_i Q_{Bi} \cdot f_{Bi} + \sum_j Q_{Fj} \cdot f_j$

$\bar{m} := \sum_i Q_{Bi} \cdot m_{Bi}$

Note that $\bar{m}$ is the average number of male gametes taken over *all* members of the population, thus including the female members, the m's of which are zero. Applying the derivations of section 3.1 analogously to the present situation of gynodioecy, one obtains for the mating frequencies in the diplophase under the assumption of random fusion of the gametes:

$$P(T_{Bi} \times T_{Bk}) = \frac{Q_{Bi} \cdot Q_{Bk} \cdot (f_{Bi} \cdot m_{Bk} + f_{Bk} \cdot m_{Bi})}{\bar{f} \cdot \bar{m}} \quad \text{for } i \neq k, \qquad (3.4a)$$

$$\begin{aligned} P(T_{Bi} \times T_{Bi}) &= \frac{Q_{Bi}^2 \cdot f_{Bi} \cdot m_{Bi}}{\bar{f} \cdot \bar{m}}, \\ P(T_{Bi} \times T_{Fj}) &= \frac{Q_{Bi} \cdot Q_{Fj} \cdot m_{Bi} \cdot f_j}{\bar{f} \cdot \bar{m}}, \end{aligned} \qquad (3.4b)$$

$$P(T_{Bi}) = \frac{1}{2} Q_{Bi} \cdot \left(\frac{f_{Bi}}{\bar{f}} + \frac{m_{Bi}}{\bar{m}} \right), \quad P(T_{Fj}) = \frac{1}{2} \frac{Q_{Fj} \cdot f_j}{\bar{f}}. \qquad (3.4c)$$

Since matings among female types are excluded, the natural mating references in the diplophase are given by $R_{Bk \triangleleft Bi} = Q_{Bk}$, $R_{Fj \triangleleft Bi} = Q_{Fj}$, and $R_{Bi \triangleleft Fj} = Q_{Bi}/Q_B$. Hence, the mating preferences are

$$U_{Bk \triangleleft Bi} = \frac{f_{Bi} \cdot m_{Bk} + f_{Bk} \cdot m_{Bi}}{f_{Bi} \cdot \bar{m} + m_{Bi} \cdot \bar{f}}, \qquad (3.5a)$$

$$U_{Fj\triangleleft Bi} = \frac{m_{Bi} \cdot f_j}{f_{Bi} \cdot \bar{m} + m_{Bi} \cdot \bar{f}} \ , \quad U_{Bi\triangleleft Fj} = \frac{m_{Bi} \cdot Q_B}{\bar{m}}, \tag{3.5b}$$

and the mating successes are

$$h_{Bi} = \frac{1}{2}\left(\frac{f_{Bi}}{\bar{f}} + \frac{m_{Bi}}{\bar{m}}\right), \quad h_{Fj} = \frac{\frac{1}{2} \cdot f_j}{\bar{f}}. \tag{3.6}$$

As was to be expected, all female types have the same pattern of mating preferences, while this holds for the cosexual types only if their female and male fertilities are proportional, i.e. if m_{Bi}/f_{Bi} is constant for all i. In this case of sexual symmetry of the cosexual types (see section 3.1), the difference $U_{Bk\triangleleft Bi} - U_{Fj\triangleleft Bi}$ is equal to $2 \cdot f_{Bk} - f_j$ with the exception of a positive factor. Female types must, therefore, produce more than twice as many ovules as cosexual types in order to induce cosexual types to prefer females over cosexuals. From this it furthermore follows immediately that *random mating among all types in the diplophase* can exist if and only if there are no differences in fertility among the cosexual nor among the female types ($f_{Bi} = f_B$, $m_{Bi} = m_B$ and $f_j = f$), and if the female type produces exactly twice as many ovules as the cosexual type ($f = 2 \cdot f_B$).

The dependence of the mating success upon sexual specificity can be demonstrated more clearly if it is assumed that neither among the cosexual types nor among the female types differences in fertility exist, i.e. if $f_{Bi} \equiv f_B$, $m_{Bi} \equiv m_B$, and $f_j \equiv f$. From equation (3.6) it then follows that

$$h_B = \frac{1}{2}\left(\frac{f_B}{f_B \cdot Q_B + f \cdot Q_F} + \frac{1}{Q_B}\right), \quad h_F = \frac{\frac{1}{2} \cdot f}{f_B \cdot Q_B + f \cdot Q_F},$$

and therefore

$$\frac{h_B}{h_F} = \frac{2 \cdot f_B}{f} + \frac{Q_F}{Q_B}. \tag{3.7}$$

Consequently, the ratio of the mating success of both sexual types is frequency dependent, and, since $Q_F + Q_B = 1$, the cosexual type is superior to the female type irrespective of the fertilities if there are more female than cosexual individuals in the population. This advantage of cosexuality may vanish only if there are fewer female than cosexual individuals in the population, and if the females produce more than twice as many ovules as the cosexuals ($f > 2 \cdot f_B$). In this case $h_F > h_B$, $h_F < h_B$, or $h_F = h_B$ hold according to whether Q_F is less than, greater than, or equal to $\frac{1}{2}(f - 2f_B)/(f - f_B)$, respectively. In this case, for given fertilities, an initial advantage of female individuals can gradually disappear as their frequency increases. As opposed to this, cosexual individuals have a mating advantage over females for all frequencies, whenever the former produce more than half as many ovules as the latter.

3.4 Trioecy

The model introduced in section 3.1 will again serve to demonstrate several of the features of this system of sexuality, which is characterized by the existence of a cosexual and two complementary unisexual (male and female) types of sexuality. Hence, random fusion of all gametic types is assumed, and the effects of this on the resulting system of mating in the diplophase will be investigated. In order to reduce the analysis to the essential aspects of this mating system, it will furthermore be stipulated that within each of the sexual types no additional distinctions are made with respect to the variation of the fertilities. The parameters in the following Table of notations do therefore suffice for treating the relevant problems

Notations

$Q_B, Q_F, Q_M :=$ relative frequency of cosexual, female, and male individuals, respectively, in the diplophase.

$f_B, m_B :=$ average number of female and male gametes, respectively, of a cosexual individual.

$f, m :=$ average number of gametes of a female and male individual, respectively.

$\bar{f} :=$ $f_B \cdot Q_B + f \cdot Q_F$, or the average female fertility among all members of the population (including males).

$\bar{m} :=$ $m_B \cdot Q_B + m \cdot Q_M$, or the average male fertility among all members of the population (including females).

On the basis of the argumentation in the last section, one obtains the following equations for the mating frequencies in the diplophase:

$$P(T_B \times T_B) = \frac{Q_B^2 \cdot f_B \cdot m_B}{\bar{f} \cdot \bar{m}},\ P(T_B \times T_F) = \frac{Q_B \cdot Q_F \cdot m_B \cdot f}{\bar{f} \cdot \bar{m}}, \quad (3.8a)$$

$$P(T_B \times T_M) = \frac{Q_B \cdot Q_M \cdot f_B \cdot m}{\bar{f} \cdot \bar{m}},\ P(T_F \times T_M) = \frac{Q_F \cdot Q_M \cdot f \cdot m}{\bar{f} \cdot \bar{m}}, \quad (3.8b)$$

$$P(T_B) = \frac{1}{2} Q_B \left(\frac{f_B}{\bar{f}} + \frac{m_B}{\bar{m}} \right),\ P(T_F) = \frac{1}{2} Q_F \frac{f}{\bar{f}},\ P(T_M) = \frac{1}{2} Q_M \frac{m}{\bar{m}}\,. \quad (3.8c)$$

The natural mating references are now $R_{B \lhd B} = Q_B$, $R_{F \lhd B} = Q_F$, $R_{M \lhd B} = Q_M$, $R_{B \lhd F} = Q_B/(1-Q_F)$, $R_{M \lhd F} = Q_M/(1-Q_F)$, $R_{B \lhd M} = Q_B/(1-Q_M)$, and $R_{F \lhd M} = Q_F/(1-Q_M)$. From this the mating preferences

$$U_{B \lhd B} = \frac{2 \cdot f_B \cdot m_B}{f_B \cdot \bar{m} + m_B \cdot \bar{f}}\,, \quad U_{F \lhd B} = \frac{m_B \cdot f}{f_B \cdot \bar{m} + m_B \cdot \bar{f}}\,, \quad (3.9a)$$

$$U_{M \lhd B} = \frac{f_B \cdot m}{f_B \cdot \bar{m} + m_B \cdot \bar{f}}\,,\ U_{B \lhd F} = \frac{m_B}{\bar{m}}(1 - Q_F)\,, \quad (3.9b)$$

$$U_{M \lhd F} = \frac{m}{\bar{m}}(1-Q_F),\ U_{B \lhd M} = \frac{f_B}{\bar{f}}(1-Q_M),\ U_{F \lhd M} = \frac{f}{\bar{f}}(1-Q_M) \quad (3.9c)$$

result. Obviously, the female sex always has the highest preference for that sexual type with the largest male fertility, and, in the same manner, the male sex prefers most the sexual type with the largest female fertility. In particular, each unisexual type can mate at random with both the other sexual types if the pertinent fertilities are identical (i.e. if $m_B = m$ or $f_B = f$, respectively). On the other hand, the cosexual type can mate at random with both unisexual types only if its two sex specific fertilities are equal to half of the fertilities of the pertinent unisexual type, i.e. if $f_B = \frac{1}{2} f$ and $m_B = \frac{1}{2} m$. *Random mating among all types in the diplophase can, therefore, under no circumstances be realized.*

As far as the mating successes of the three sexual types are concerned, one obtains

$$h_B = \frac{1}{2} \left(\frac{f_B}{\bar{f}} + \frac{m_B}{\bar{m}} \right), \quad h_F = \frac{\frac{1}{2} f}{\bar{f}}\,, \quad h_M = \frac{\frac{1}{2} m}{\bar{m}}\,, \quad (3.10)$$

and therefore

$$\frac{h_B}{h_F} = \frac{f_B}{f} + \frac{m_B}{f} \cdot \frac{\bar{f}}{\bar{m}} \,, \quad \frac{h_B}{h_M} = \frac{m_B}{m} + \frac{f_B}{m} \cdot \frac{\bar{m}}{\bar{f}} \,, \quad \frac{h_M}{h_F} = \frac{m}{f} \cdot \frac{\bar{f}}{\bar{m}} \,.$$

All three quotients are again frequency dependent, and, in particular, for arbitrary but fixed frequency Q_B of cosexual individuals, $\bar{f}/\bar{m}$ is an increasing function of Q_F (and thus a decreasing function of Q_M). Hence, for a given value of Q_B, h_B/h_F and h_M/h_F increase with Q_F, and h_B/h_M increases with Q_M. For gynodioecy (Q_M close to 0) the cosexual type thus gains its greatest relative advantage in mating success over the female type, and it is relatively most inferior to the male type. With androdioecy (Q_F close to 0), the opposite holds true. Consequently, the superiority in mating success of one sexual type over another is frequency dependent in a complicated way as long as no restricting assumptions are imposed on the mating system, i.e. on the fertilities in the present model.

With respect to their mating successes, a comparison of random mating (in the diplophase) of the unisexual types with random mating of the cosexual type is here particularly interesting (recall that random mating among all three sexual types is impossible). In fact, this corresponds to a situation where different systems of sexuality practice random mating with each other (the dioecious system mates at random with the cosexual system or vice versa), and it deserves separate treatment:

▷ *Random mating of both unisexual sexes* is realized if and only if $m_B = m$ (random mating of the females) and $f_B = f$ (random mating of the males). In this case the quotients of the mating successes become

$$\frac{h_B}{h_F} = 1 + \frac{1 - Q_M}{1 - Q_F} \,, \quad \frac{h_B}{h_M} = 1 + \frac{1 - Q_F}{1 - Q_M} \,, \quad \frac{h_M}{h_F} = \frac{1 - Q_M}{1 - Q_F} \,.$$

Thus, the cosexual type is globally superior (under all frequency conditions) in mating success to both unisexual types. The relationship between the two unisexual types is characterized by a negative frequency dependence, since the more frequent of the two sexes is always inferior in mating success to the less frequent.

▷ *Random mating of the cosexual type* is equivalent to $f_B = \frac{1}{2}f$ and $m_B = \frac{1}{2}m$. The quotients of the mating successes are now

$$\frac{h_B}{h_F} = \frac{1}{2}\left(1 + \frac{\frac{1}{2}Q_B + Q_F}{\frac{1}{2}Q_B + Q_M}\right) \,, \quad \frac{h_B}{h_M} = \frac{1}{2}\left(1 + \frac{\frac{1}{2}Q_B + Q_M}{\frac{1}{2}Q_B + Q_F}\right) \,,$$

$$\frac{h_M}{h_F} = \frac{\frac{1}{2}Q_B + Q_F}{\frac{1}{2}Q_B + Q_M} \ .$$

As was the case in the previous situation, the unisexual sexes show negative frequency dependence among each other in that the more frequent is automatically the less successful sex. In contrast, the cosexual type takes an intermediate position, since its mating success is always placed between that of the two unisexual types.

In both these cases random mating is seen to have quite different consequences for the mating success: while random mating of both unisexual types confers an unrestricted advantage to the cosexual type, random mating of the cosexual type does not confer such an unrestricted advantage to its dioecious counterpart, since only one of the two unisexual types can be superior to the cosexual type at a time.

4. Evolution of systems of sexuality

Evolution is the change in genotypic frequencies. A change in phenotypic frequencies can be considered as an evolutionary event only if these phenotypes are subject to at least partial genetic control. Phenotypic variation due to causes which are not attributable to genetic variation cannot evolve, since it is not heritable and therefore solely due to the respective environmental conditions. The evolution of particular characteristics, such as sexual specificity, requires that they be heritable. Depending on the mode of inheritance, evolution may proceed along very different pathways. Thus, the evolutionary success of a sexual type or even whole systems of sexuality need not be completely determined by the absolute or relative reproductive success of the types; the mode of inheritance may also exert a decisive influence. This does not, of course, rule out the existence of particular modes of inheritance which translate reproductive success into evolutionary success, i.e. under the action of which the reproductive advantage (measured by the mating success) of a type guarantees that it will increase in frequency over the course of generations.

In the following examples, which are designed to illustrate the evolution of systems of sexuality, such modes of inheritance (translating reproductive into evolutionary success) will be given priority. To prevent unjustifiable generalizations, a brief example for a mode of inheritance will be given that cancels out to a large degree the effects of differential reproductive success. However, it is beyond the scope of this treatise to discuss and speculate on the relative importance of reproductive success versus mode of inheritance for our understanding of evolutionary phenomena, even though this very interesting topic has as yet not received the attention which it possibly deserves.

As the primary system of mating, random fusion of gametic types will again be assumed, so that the models on gynodioecy, androdioecy, and trioecy treated in the preceding section apply. Moreover, natural mating references based on the relative frequencies of the types in the population will be considered exclusively. This is indispensable, since evolutionary events appear as changes in frequency of the types over the generations. These generations are supposed to be separated in the sense that at any time all members of the population are of the same age. Furthermore, it has to be taken into account that measurements of fertility must always cover the period of time reaching from the production of gametes back to the stage at which the relative frequencies of the types serving as mating reference were scored. The earlier this stage is chosen prior to the actual production of gametes, the more effects of differential viability will enter into the measurement of fertilities. Individuals which do not survive to the stage of sexual maturity will thus have to be assigned a fertility of zero. A lower probability for an individual of a type to survive from the stage of census to the stage of sexual maturity therefore proportionately decreases the mean male and female fertility of this type.

The mode of inheritance becomes manifest in the frequencies with which certain types appear among the offspring of a particular mating type. Since now the typification refers to the genotypes of the individuals, the mode of inheritance can, at least ideally, be specified by the genotypic frequencies that are realized in the zygotic output of the single mating types. Consequently, the zygotic stage represents the stage of census for the measurement of fertilities and frequencies of types in all successive generations, and evolutionary events are observed as changes of frequencies in this stage. The majority of the models treated subsequently will be based on this description.

4.1 Gynodioecy

The simplest genetic mechanism which can code for this system of sexuality consists of two alleles A_1 and A_2 at a diploid gene locus, where one of the alleles, A_2 say, has the effect of suppressing or modifying the potential for the production of male gametes. Thus, individuals possessing the allele A_2 would have to be classified as females or male steriles. Depending on whether the effect of A_2 is dominant or recessive, one usually distinguishes between **dominant and recessive gynodioecy**. Hence, for dominant gynodioecy A_1A_1-individuals are cosexual, while both A_1A_2- and A_2A_2-individuals belong to the female sex. On the other hand, for recessive gynodioecy, A_1A_1- and A_1A_2-individuals are cosexual and A_2A_2-individuals are female. The evolutionary characteristics of these two forms of gynodioecy will now be considered separately in order to point out possible differences.

Dominant gynodioecy: The notations describing this mode of inheritance are summarized in the following table:

Notations

Sexual type	⚥	♀	♀
Genotype	A_1A_1	A_1A_2	A_2A_2
Fertility	f_B, m_B	f	f
Frequency	$Q_{11} = Q_B$	$Q_{12} = Q_F$	Q_{22}

The relative frequencies Q refer to the zygotic stage of the respective generation, and the notation Q' will be used to indicate the next generation. Since in all generations after the first, the genotype A_2A_2 cannot arise from any of the admissible matings, $Q_{22} = 0$ will be assumed from the beginning, so that only the genotypes A_1A_1 and A_1A_2 appear with frequencies Q_B and Q_F, respectively ($Q_B + Q_F = 1$). Under the assumption of regular segregation of the two alleles in the zygote production of each mating type, one obtains for the frequency Q'_B of cosexuals and $Q'_F = 1 - Q'_B$ of females in the next generation:

$$Q'_B = P(T_B \times T_B) + \frac{1}{2}P(T_B \times T_F) = P(T_B),$$

$$Q'_F = \frac{1}{2}P(T_B \times T_F) = P(T_F).$$

Consequently,

$$\frac{Q'_B}{Q'_F} = \frac{P(T_B)}{P(T_F)} = \frac{h_B}{h_F} \cdot \frac{Q_B}{Q_F},$$

i.e. the sex ratio Q_B/Q_F of the two sexual types changes over the generations proportional to the ratio h_B/h_F of the mating successes. Replacing h_B/h_F in the above equation by equation (3.7) yields

$$\frac{Q'_B}{Q'_F} = \frac{2f_B}{f} \cdot \frac{Q_B}{Q_F} + 1.$$

For $2f_B = f$, the solution of the above difference equation shows that after t generations

$$\frac{Q_B(t)}{Q_F(t)} = \frac{Q_B}{Q_F} + t\ .$$

Thus, in this case the sex ratio increases without being bounded from above, so that the female sexual type vanishes asymptotically. On the other hand, if $2f_B \neq f$, the solution of the difference equation has the form

$$\frac{Q_B(t)}{Q_F(t)} = \left(\frac{2f_B}{f}\right)^t \cdot \left(\frac{Q_B}{Q_F} - \frac{f}{f-2f_B}\right) + \frac{f}{f-2f_B} \ .$$

Consequently, for $f > 2f_B$ the sex ratio converges in the course of the generations to the limit $f/(f-2f_B)$, while for $f < 2f_B$ it again increases without reaching a bound. Therefore, stable coexistence of both sexual types requires $f > 2f_B$, and in the equilibrium state approached, cosexual individuals are always more frequent than females. The following Table summarizes this.

Result

Under the assumption of random fusion of the gametes, dominant gynodioecy can evolve only if an average female individual produces more than twice as many female gametes as an average cosexual individual. In this case, the sex ratio ⚥ : ♀ equals $f/(f-2f_B)$ *at equilibrium, so that cosexual individuals are always more frequent than female (male sterile) individuals.*

Dominant gynodioecy can evolve only if, for low frequency of the female, the average female individual is superior to an average cosexual individual in mating success. Evolutionary and reproductive success are therefore in accordance. This is also supported by the mating preferences of the cosexual type, since $U_{F \triangleleft B} > U_{B \triangleleft B}$ allows for the evolution of gynodioecy, while $U_{F \triangleleft B} \leq U_{B \triangleleft B}$ prevents it (consult the equations (3.5)).

Recessive gynodioecy: The assignment of the sexual types to the three genotypes now is as follows:

Notations

Sexual type	⚥	⚥	♀
Genotype	A_1A_1	A_1A_2	A_2A_2
Fertility	f_B, m_B	f_B, m_B	f
Frequency	Q_{11}	Q_{12}	Q_F

In order to arrive at a representation of the transition equations which is as simple as possible, the relative allele frequency $q_1 := Q_{11} + \frac{1}{2}Q_{12}$ of A_1 will be introduced. Hence, the relative allele frequency of A_2 is given by $q_2 := 1 - q_1$. Since, with the help of the thus defined allele frequency, the frequencies of the two cosexual genotypes can be written as $Q_{12} = 2(1 - q_1 - Q_F)$ and $Q_{11} = 2q_1 + Q_F - 1$, all genotypic frequencies are uniquely specified by q_1 and Q_F. In the next generation these two frequencies are

$$q_1' = P(T_{11}) + \frac{1}{2}P(T_{12}), \quad Q_F' = \frac{1}{4}P(T_{12} \times T_{12}) + \frac{1}{2}P(T_{12} \times T_F),$$

and, using the mating frequencies obtained in section 3.3 for gynodioecy:

$$q_1' = q_1 \cdot \frac{f_B(1 - Q_F) + \frac{1}{2}fQ_F}{\bar{f}(1 - Q_F)} \quad \text{with} \quad \bar{f} = f_B(1 - Q_F) + fQ_F,$$

$$Q_F' = \frac{1}{2}Q_{12} \cdot \frac{\frac{1}{2}f_BQ_{12} + fQ_F}{\bar{f}(1 - Q_F)} = (1 - Q_F - q_1) \cdot \frac{f_B(1 - Q_F - q_1) + fQ_F}{\bar{f}(1 - Q_F)}.$$

Rewriting the transition equation for q_1 in the form

$$\frac{q_1'}{q_1} - 1 = \frac{Q_F}{1 - Q_F} \cdot \frac{f_B - \frac{1}{2}f + (f - f_B)Q_F}{f_B + (f - f_B)Q_F} \ ,$$

the numerator of the second fraction on the right side is an increasing or decreasing function of Q_F depending on whether $f > f_B$ or $f < f_B$, respectively. Clearly, for $f_B \geq \frac{1}{2}f$ and $Q_F > 0$ this numerator is always positive, in which case $q_1'/q_1 > 1$. Hence, the condition $f_B \geq \frac{1}{2}f$ implies that the frequency of A_1 converges to 1 over the course of the generations, so that the female sex gradually disappears and the population becomes purely cosexual.

If, on the other hand, $f_B < \frac{1}{2}f$, then the frequency of A_1 will increase over the generations as long as $Q_F > (\frac{1}{2}f - f_B)/(f - f_B)$. Hence, *with respect to the conditions for establishment and the equilibrium sex ratio recessive and dominant gynodioecy are the same* (note that the sex ratio ⚥ : ♀, i.e. $(1 - Q_F)/Q_F$, at equilibrium is for both modes of inheritance equal to $f/(f - 2f_B)$). The differences between the two forms of gynodioecy primarily lie in the dynamics around the internal equilibrium.

The above results on the evolution of dominant and recessive gynodioecy apply analogously to the evolution of (dominant and recessive) androdioecy. One only has to replace the female by the male sex for all of the model parameters concerned, so that f becomes m and Q_F becomes

Q_M. The first studies of these model types are probably due to Ross and Weir (1975, 1976).

4.2 Trioecy

Particularly in studies of the evolution of dioecy, trioecy plays a crucial role. This becomes obvious from the fact that the clear majority of higher organisms is either genuinely cosexual or dioecious, and that, therefore, evolutionary pathways from one to the other of these two sexual systems must necessarily have passed through transient states of trioecy. Hence, depending on its mode of inheritance and reproduction, trioecy may hinder or advance the evolution of dioecy from cosexuality or vice versa.

As a rule, dioecy is inherited by the well-known X–Y mechanism, which is tantamount to a genetic control by two alleles at a single gene locus. One of the sexes is homogametic (homozygous) and the other is heterogametic (heterozygous), and due to unisexuality the second (theoretically possible) homozygous genotype cannot be formed. The simplest mode of inheritance of trioecy would thus be realized if this second homozygous genotype, if it existed, would code for cosexuality. Under the assumption of *male heterogamety* this would give rise to the following system:

Notations

Sexual type	⚥	♂	♀
Genotype	A_1A_1	A_1A_2	A_2A_2
Fertility	f_B, m_B	m	f
Frequency	Q_B	Q_M	Q_F

For this mode of inheritance of trioecy the implicit "marginal" systems of sexuality are cosexuality (with $Q_B = 1$), dioecy (with $Q_B = 0$), and (dominant) androdioecy (with $Q_F = 0$). If male heterogamety is replaced by female heterogamety (♀ $= A_1A_2$), then (dominant) gynodioecy takes the place of androdioecy as a marginal system of sexuality. Since, under the assumption of random fusion of the gametes, male and female heterogamety have evolutionarily analogous consequences, the following treatment will be restricted to male heterogamety.

The transition equations for the frequencies of the three sexual types are now

$$\begin{aligned}
Q'_B =& P(T_B \times T_B) + \frac{1}{2}P(T_B \times T_M),\\
Q'_M =& P(T_B \times T_F) + \frac{1}{2}P(T_B \times T_M) + \frac{1}{2}P(T_M \times T_F),\\
Q'_F =& \frac{1}{2}P(T_M \times T_F).
\end{aligned}$$

It immediately turns out that after the first generation $Q_F \leq \frac{1}{2}$ and $Q_F \leq Q_M$. Replacing the mating frequencies by the equations (3.8) one obtains:

$$\begin{aligned}
Q'_B =& Q_B f_B \cdot \frac{Q_B m_B + \frac{1}{2}Q_M m}{\bar{f} \cdot \bar{m}} \ ,\\
Q'_M =& \frac{\frac{1}{2}Q_B Q_M f_B m + Q_F f(Q_B m_B + \frac{1}{2}Q_M m)}{\bar{f} \cdot \bar{m}} \ ,\\
Q'_F =& Q_F \cdot \frac{\frac{1}{2}Q_M f m}{\bar{f} \cdot \bar{m}} \ ,
\end{aligned}$$

where $\bar{f} = Q_B f_B + Q_F f$ and $\bar{m} = Q_B m_B + Q_M m$.

To facilitate the analysis of the different possibilities of evolution, the dynamics of trioecy will be considered in the close vicinity of each of the three marginal systems of sexuality (see Gregorius et al. 1983). The equilibrium frequencies in any of the marginal systems will be denoted by $\hat{Q}$. Clearly, in the case of dioecy $\hat{Q}_F = \hat{Q}_M = \frac{1}{2}$. For androdioecy as a marginal system the results on dominant gynodioecy derived in section 4.1 can be used after translation into its androdioecious equivalent. Thus, androdioecy exists as a marginal system of trioecy if $m > 2m_B$, and the equilibrium frequencies are given by $\hat{Q}_B = \frac{1}{2}m/(m - m_B)$ and $\hat{Q}_M = 1 - \hat{Q}_B$. If, on the other hand, $m \leq 2m_B$, then cosexuality ($\hat{Q}_B = 1$) is the only marginal system of sexuality that exists in addition to dioecy.

Let α_B be the limit to which Q'_B/Q_B converges as Q_B approaches 0 and both Q_F and Q_M approach $\frac{1}{2}$. The limit $\alpha_B = f_B/f$ is directly obtained from the above transition equations. In case $\alpha_B < 1$, this would imply that the proportion of cosexual individuals decreases from generation to generation if it started at a sufficiently low frequency, and, consequently, the cosexual type disappears asymptotically from the population.

Thus, for $\alpha_B < 1$ dioecy is at least a locally stable system of sexuality. Conversely, for $\alpha_B > 1$ the cosexual type will increase in frequency when rare, and dioecy would thus be unstable. In the present model $f_B < f$ is therefore a necessary prerequisite for the evolution of dioecy while $f_B > f$ prevents it.

In the same manner, the quantity α_F is defined as the limit of Q'_F/Q_F as Q_F approaches 0 and both Q_B and Q_M approach the equilibrium values of the marginal systems of cosexuality or androdioecy, respectively. The transition equations show that for $m \leq 2m_B$ (marginal system cosexuality) $\alpha_F = 0$, and for $m > 2m_B$ (marginal system androdioecy with $\hat{Q}_B = \frac{1}{2}m/(m - m_B)$ and $\hat{Q}_M = 1 - \hat{Q}_B$) $\alpha_F = f(m - 2m_B)/(mf_B)$. For $m \leq 2m_B$ pure cosexuality is thus locally stable. For $m > 2m_B$ cosexuality is unstable and leads to locally stable or unstable androdioecy depending on whether $\alpha_F < 1$ or $\alpha_F > 1$, respectively.

In order to guarantee the coexistence of all three sexual types (and thus the stability of trioecy, not necessarily the stability of internal sex ratio equilibria), all three marginal systems are required to be simultaneously unstable (repelling), so that $\alpha_B \geq 1$ and $\alpha_F \geq 1$ would be the pertinent necessary conditions. However, these two conditions can never be realized simultaneously, as is easily seen. In the present model, trioecy is therefore a system of sexuality that has a primarily transient function in that it lays the basis for the evolution of any of the three marginal systems of sexualtity. In particular, the instability of one marginal system of sexuality provides the conditions for the evolution of another (at least locally) stable marginal system. For example, $\alpha_F > 1$ and $\alpha_B < 1$ are the preconditions for the evolution of dioecy from cosexuality. In detail, one arrives at the results stated in the following Table.

Result

For random fusion of the gametes and under the above-specified mode of inheritance, trioecy is an evolutionarily transient system of sexuality.

(a) Dioecy may evolve from cosexuality or from androdioecy if the male sex produces per individual more than twice as many male gametes as the cosexuals ($m > 2m_B$) and if the ratio in the production of female gametes between the cosexual and female sex meets the inequality $f_B/f < (m - 2m_B)/m$.

(b) Cosexuality may evolve from dioecy if the cosexuals produce per individual more female gametes than the female sex and not less than half of the male gametes of the male sex ($f_B > f$ and $m_B \geq \frac{1}{2}m$).

(c) Androdioecy may evolve from dioecy if the cosexuals produce per individual more female gametes than the female sex and less than half of the male gametes of the male sex ($f_B > f$ and $m_B < \frac{1}{2}m$).

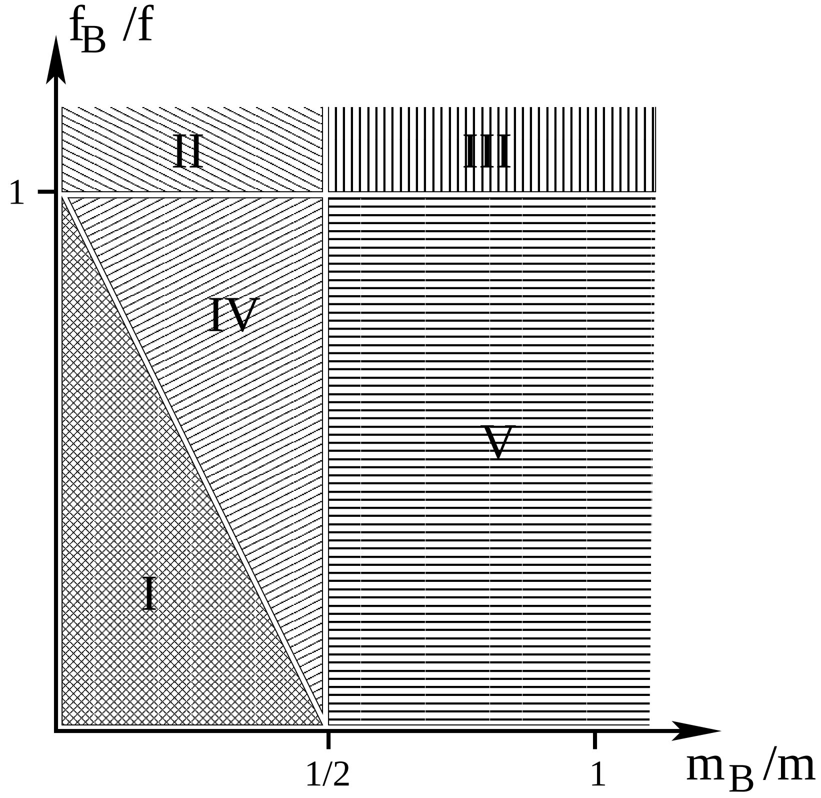
Figure 1 illustrates the regions of fertility ratios (cosexual versus unisexual) which allow for the evolution of the various marginal systems of sexuality including facultative evolution. By **facultative evolution** it is understood that different marginal systems of sexuality can evolve for the same set of fertilities if the population starts with different initial frequencies of the sexual types. This situation is characterized by local stability of more than one marginal system, and it prevents the establishment of any system other than the prevailing system. The figure is self-explanatory.

In contrast with the previous results on gynodioecy and androdioecy, reproductive success is now not necessarily associated with evolutionary success. This can be easily seen from the mating successes computed in section 3.4 (cf. equation (3.10)). For example, simple superiority of the cosexual type over both unisexual types in mating success is not sufficient to guarantee evolution of cosexuality from dioecy. Instead, the mating preferences (see equations (3.9)) turn out to be more reliable predictors of evolutionary success:

(a) Dioecy may evolve from cosexuality or androdioecy if

$$\frac{U_{B \triangleleft M}}{U_{F \triangleleft M}} < 1 - \frac{U_{B \triangleleft B}}{U_{M \triangleleft B}} \; .$$

Figure 1



Regions of cosexual:unisexual fertility ratios allowing for the evolution of various marginal systems of sexuality. f_B, m_B = *female and male fertility of cosexuals;* f, m = *fertilities of females and males. I: Evolution of dioecy from cosexuality or androdioecy; II: Evolution of androdioecy from dioecy; III: Evolution of cosexuality from dioecy or androdioecy; IV: Facultative evolution of dioecy or androdioecy; V: Facultative evolution of dioecy or cosexuality.*

(b) Cosexuality may evolve from dioecy if

$$U_{B \triangleleft M} > U_{F \triangleleft M} \quad \text{and} \quad U_{B \triangleleft B} \geq U_{M \triangleleft B} \ .$$

(c) Androdioecy may evolve from dioecy if

$$U_{B \triangleleft M} > U_{F \triangleleft M} \quad \text{and} \quad U_{B \triangleleft B} < U_{M \triangleleft B}.$$

Thus, the evolution of dioecy requires that the male sex show a stronger mating preference for the female than for the cosexual sex, and that, furthermore, the self-preference of the cosexuals be sufficiently lower than for the male sex. The other two cases allow for an analogous interpretation.

Cosexuals heterozygous: A change in the mode of inheritance of trioecy — even if it occurs only within the presently considered two-allele system — may have consequences that deviate considerably from the above. This shows up immediately when the cosexual type is assumed to be heterozygous, so that the two unisexual types are homozygous for the different alleles:

Notations

Sexual type	♂	⚥	♀
Genotype	A_1A_1	A_1A_2	A_2A_2

One recognizes immediately that all three genotypes must persist in the population, since each homozygous individual can mate only with individuals that differ from it in genotype. The evolutionary emergence of such a mode of inheritance is probably difficult to explain, and it requires consideration of additional alleles, gene loci, or gene-cytoplasmic interactions. However, this mode of inheritance is not claimed to be of any specific biological relevance (trioecy is anyway a very seldomly observed system, and its genetics are almost unknown); it is rather intended for demonstration of a case where changes in the mode of inheritance may turn a previously completely unstable trioecious system of sexuality into its other extreme, namely a completely stable system. It is also noticeable that the stability of trioecy resulting from the heterozygosity of the cosexual type cannot be endangered by arbitrary changes in the fertilities; only the equilibrium sex ratios will be affected by such changes.

5. Self-mating or self-fertilization

5.1 Functional sex and self-mating proportions

As a rule, higher organisms are characterized by a gametic dimorphism which allows distinction between female (receptor) and male (donor) gametes. If mating is defined by the fusion of gametes, each cosexual individual can perform matings in which it functions as male or/and as female. In general, these two sex functions need not be realized in equal proportions among the matings performed. Extending this idea from single individuals to whole types, it is meaningful to characterize even in a dioecious population each type with respect to the male and female function it displays in the matings. Only if the typification includes the (unisexual) sexual type as a component, each type can display only one of the two sex functions. In any case, the **functional sex** of a type or individual can be quantified by considering only those gametes involved in matings (fusions) and expressing the female gametes of all individuals of a type as a fraction of all gametes (male *and* female) of individuals of this type (cf. Ross and Gregorius 1983). The thus defined functional sex will be denoted by Φ_i for the i-th type, and it assumes values ranging from 0 to 1. $\Phi_i = 0$ indicates that the i-th type functions as a genuine male, while $\Phi_i = 1$ indicates a type that functions as a genuine female. The "ideal" cosexual function would then correspond to $\Phi_i = \frac{1}{2}$, and deviations upward and downward would reveal tendencies for increased female or male function, respectively, of the type.

To arrive at a formal representation of Φ, each gamete will again be characterized by its sexual specificity (F or M) and by the type T_i of its producer. Gametes are thus subject to the typification T_{Fi} or T_{Mi}, and their frequencies $P(T_{Fi} \times T_{Mj})$ of fusion determine the mating frequencies $P(T_i \times T_j)$ of their producers according to the already known equations (3.2), i.e.

$$P(T_i \times T_j) = P(T_{Fi} \times T_{Mj}) + P(T_{Fj} \times T_{Mi}) \quad \text{for } i \neq j, \text{ and}$$

$$P(T_i \times T_i) = P(T_{Fi} \times T_{Mi}).$$

The relative mating participation of T_i-individuals as males and females is therefore $P(T_{Mi})$ and $P(T_{Fi})$, respectively, the sum of which is $P(T_{Mi}) +$

$P(T_{Fi}) = P(T_i)$. The desired formal representation of the functional sex of the type T_i thus has the form

$$\Phi_i = \frac{P(T_{Fi})}{P(T_i)} \ . \tag{5.1}$$

In connection with the development of the concept of mating equivalence, the proportion of self-mating P_i^s of a type T_i was introduced in section 1.5, where it was defined as the relative frequency of individual self-matings among all matings performed by T_i-individuals. This self-mating proportion can be further decomposed into a female and male component when matings are defined as the fusion of gametes, so that individual self-mating is equivalent to the common notion of self-fertilization. The distinction between female and male function in matings thus allows us to consider the following sex-specific proportions:

Notations

P_{Fi}^s := the proportion of individual self-matings (self-fertilizations) among all female gametes involved in matings (fertilizations) and produced by T_i-individuals (**female self-mating proportion**);

P_{Mi}^s := the proportion of individual self-matings among all male gametes involved in matings and produced by T_i-individuals (**male self-mating proportion**).

Since the number of female and male gametes involved in self-fertilizations of an individual must always be identical, the three proportions of self-mating or self-fertilization depend upon each other according to the equations

$$P_{Fi}^s \cdot P(T_{Fi}) = P_{Mi}^s \cdot P(T_{Mi}) = \frac{1}{2} P_i^s \cdot P(T_i) \ , \tag{5.2}$$

so that the two sex-specific self-mating proportions and the combined (overall) self-mating proportion are connected by the relationship

$$P_i^s = \frac{2 \cdot P_{Fi}^s \cdot P_{Mi}^s}{P_{Fi}^s + P_{Mi}^s} \ . \tag{5.3}$$

Consequently,

Result

The (combined) self-mating proportion of a type is equal to the harmonic mean of its female and male self-mating proportion.

If a type practices self-mating (i.e. if $P_i^s > 0$), a remarkable relationship exists between its functional sex and its self-mating proportions. Multiplying the numerator of Φ_i by P_{Fi}^s and applying the above equations (5.2) and (5.3) yields

$$\Phi_i = \frac{\frac{1}{2}P_i^s}{P_{Fi}^s} = \frac{P_{Mi}^s}{P_{Fi}^s + P_{Mi}^s} \ . \tag{5.4}$$

Hence, even though the original definition of Φ_i involves neither the concept nor any measures of self-mating, it nevertheless turns out that:

Result

The functional sex of a type or individual practicing self-mating is completely specified by its two sex-specific proportions of self-mating.

In particular, one recognizes that only for "ideal" cosexuality, i.e. $\Phi_i = \frac{1}{2}$, all three proportions of self-mating assume the same value. For predominant female function ($\Phi_i > \frac{1}{2}$) the male exceeds the female proportion of self-mating, while the reverse holds true for $\Phi_i < \frac{1}{2}$.

5.2 Self-mating and random cross-mating

A major objective of this section will consist in the study of the consequences of differential proportions of self-mating for mating success in cosexual populations. Hence, in order to avoid obscurance of these consequences, effects on mating success that originate from cross-mating have to be excluded. As was repeatedly emphasized in the previous sections 2.1, 2.2, and 2.3, random mating does not affect mating success provided the measurement of mating preferences is based on natural mating references and that these references are in turn based on the frequencies of the types in the population. Thus, if the objective is to study effects on mating success that originate exclusively from differential proportions of self-mating, it has to be assumed that all cross-matings occur at random. This assumption underlies the following considerations.

Mating on the level of the individual: The relationships between mating norms ($P_{i\triangleleft j}$), cross-mating norms ($P^c_{i\triangleleft j}$), and self-mating proportions (P^s_i) were demonstrated in the section 1.5 about mating equivalence (see equation (1.4)):

$$P^c_{i\triangleleft j} = \frac{P_{i\triangleleft j} - \delta_{ij} \cdot P^s_j}{1 - P^s_j} \ .$$

For genuine cosexuality, the natural cross-mating references take on the form $R^c_{i\triangleleft j} = R^c_i$, so that random cross-mating is defined by $P^c_{i\triangleleft j} = R^c_i$. Applying the above equations for the cross-mating norms in connection with equation (1.1), one obtains

$$\begin{aligned} \frac{1}{2} P(T_i \times T_j) &= R^c_i \cdot (1 - P^s_j) \cdot P(T_j) \quad \text{for } i \neq j, \text{ and} \\ P(T_i \times T_i) &= [R^c_i \cdot (1 - P^s_i) + P^s_i] \cdot P(T_i). \end{aligned}$$

The fraction of self-matings among all matings performed in the population is $P^s = \sum_i P^s_i \cdot P(T_i)$. Taking this into consideration, summation of the last equation over j therefore yields:

$$P(T_i) = R^c_i \cdot (1 - P^s) + P^s_i \cdot P(T_i) \ , \text{ and thus } P(T_i) \cdot (1 - P^s_i) = R^c_i \cdot (1 - P^s).$$

This equation allows expression of the mating frequencies as functions solely of the proportions of self-mating and the cross-mating references, provided that none of the types practices complete self-mating (i.e. $P^s_i < 1$ for all i):

$$\begin{aligned} P(T_i \times T_j) &= 2 \cdot R^c_i \cdot R^c_j \cdot (1 - P^s) \quad \text{for } i \neq j, \\ P(T_i \times T_i) &= R^c_i \cdot (1 - P^s) \cdot \left(R^c_i + \frac{P^s_i}{1 - P^s_i} \right) \\ 1 - P^s &= \left(\sum_i \frac{R^c_i}{1 - P^s_i} \right)^{-1} . \end{aligned} \tag{5.5}$$

It is obvious that differences in proportions of self-mating between the types emerge here only in the homotypic matings $T_i \times T_i$. Hence, for given cross-mating references, the frequencies of heterotypic matings are not affected by any changes in the proportions of self-mating that do not alter the proportion P^s of self-matings in the total population.

Let Q_i again be the relative frequency of T_i-individuals in the population, so that $h_i = P(T_i)/Q_i$ is the mating success of this type. By the equation preceding (5.5) one then obtains for the mating success of a type that does not practice complete self-mating ($P_i^s < 1$):

$$h_i = \frac{R_i^c}{Q_i} \cdot \frac{1 - P^s}{1 - P_i^s}. \tag{5.6}$$

The differences between the h_i's now depend critically on the factors determining the cross-mating references R_i^c. For example, if the extent of self-mating of the individuals has no effect on their availability for cross-mating, then this is equivalent to $R_i^c = Q_i$ for all types, and the mating success is thus positively correlated with the proportion of self-mating, i.e. the type with the larger proportion of self-mating is also superior in mating success.

This effect of the proportions of self-mating on mating success disappears if $h_i = 1$ and, therefore, $P(T_i) = Q_i$ for all i. In this case $R_i^c = Q_i(1 - P_i^s)/(1 - P^s)$ and $\sum_i Q_i P_i^s = P^s$ $(= \sum_i P(T_i) P_i^s)$, so that the availability of the individuals of a given type as potential cross-mating partners corresponds to the frequency with which this type is involved in cross-matings. It is evident that only for this mating reference differential proportions of self-mating do not affect the mating success.

Mating on the level of the gametes: In this case mating between individuals is defined by fusion of their gametes, so that each single fusion counts as a mating event. Hence, the considerations of the last section apply. The cross-mating norms as specified in equation (1.4) are now

$$P^c_{Fi \triangleleft Mj} = \frac{P_{Fi \triangleleft Mj} - \delta_{ij} \cdot P^s_{Mj}}{1 - P^s_{Mj}} \quad \text{and} \quad P^c_{Mj \triangleleft Fi} = \frac{P_{Mj \triangleleft Fi} - \delta_{ij} \cdot P^s_{Fi}}{1 - P^s_{Fi}}.$$

Since the natural cross-mating references are R^c_{Fi} and $R^c_{Mj \triangleleft Fi} = R^c_{Mj}$, random cross-mating (cross-fertilization) among the gametes is characterized by the equations $P^c_{Fi \triangleleft Mj} = R^c_{Fi}$ and $P^c_{Mj \triangleleft Fi} = R^c_{Mj}$. The mating frequencies on the level of the gametes are therefore

$$\begin{aligned} \frac{1}{2} P(T_{Fi} \times T_{Mj}) &= \delta_{ij} \cdot P^s_{Mj} \cdot P(T_{Mj}) + R^c_{Fi} \cdot (1 - P^s_{Mj}) \cdot P(T_{Mj}) \\ &= \delta_{ij} \cdot P^s_{Fi} \cdot P(T_{Fi}) + R^c_{Mj} \cdot (1 - P^s_{Fi}) \cdot P(T_{Fi}). \end{aligned} \tag{5.7}$$

Subtracting these two expressions on the right side from each other and taking advantage of the relationship $P^s_{Mi}P(T_{Mi}) = P^s_{Fi}P(T_{Fi}) = \frac{1}{2}P^s_i P(T_i)$, it follows that

$$R^c_{Fi}(1 - P^s_{Mj})P(T_{Mj}) = R^c_{Mj}(1 - P^s_{Fi})P(T_{Fi}),$$

and after summation over j and i, respectively:

$$\begin{aligned} P(T_{Fi}) \cdot (1 - P^s_{Fi}) &= \frac{1}{2}R^c_{Fi} \cdot (1 - P^s), \\ P(T_{Mj}) \cdot (1 - P^s_{Mj}) &= \frac{1}{2}R^c_{Mj} \cdot (1 - P^s). \end{aligned} \tag{5.8}$$

Adding these two equations for $i = j$ then yields

$$P(T_i) \cdot (1 - P^s_i) = \frac{1}{2}(R^c_{Fi} + R^c_{Mi}) \cdot (1 - P^s). \tag{5.9}$$

Moreover, insertion of these into the above equations (5.7) for the mating frequencies results in

$$\begin{aligned} P(T_{Fi} \times T_{Mj}) &= R^c_{Fi} \cdot R^c_{Mj} \cdot (1 - P^s) \quad \text{for } i \neq j, \\ P(T_{Fi} \times T_{Mi}) &= \left[\frac{1}{2}(R^c_{Fi} + R^c_{Mi}) \cdot \frac{P^s_i}{1 - P^s_i} + R^c_{Fi} \cdot R^c_{Mi}\right] \cdot (1 - P^s), \end{aligned} \tag{5.10a}$$

as well as

$$1 - P^s = \left(\sum_i \frac{\frac{1}{2}(R^c_{Fi} + R^c_{Mi})}{1 - P^s_i}\right)^{-1}. \tag{5.10b}$$

It is conspicuous that only the P^s_i's but not their sexual-specific components P^s_{Fi} and P^s_{Mi} have an influence on the mating frequencies, and that, furthermore, differences between the proportions of self-mating become directly effective only within the homotypic matings $T_{Fi} \times T_{Mi}$.

Translation of the mating frequencies of gametic types into those of the producers of these gametic types yields

$$\begin{aligned} P(T_i \times T_j) &= (R^c_{Fi} \cdot R^c_{Mj} + R^c_{Fj} \cdot R^c_{Mi}) \cdot (1 - P^s) \quad \text{for } i \neq j, \\ P(T_i \times T_i) &= P(T_{Fi} \times T_{Mi}) \quad \text{as in (5.10).} \end{aligned} \tag{5.11}$$

By equation (5.9) the mating success is now

$$h_i = \frac{\frac{1}{2}(R_{Fi}^c + R_{Mi}^c)}{Q_i} \cdot \frac{1 - P^s}{1 - P_i^s} \quad , \tag{5.12}$$

which corresponds to the mating success considered on the level of the individual (see equation (5.6)) via the identity $R_i^c = \frac{1}{2}(R_{Fi}^c + R_{Mi}^c)$. Based on this identity, all of the above remarks on the effects of differential proportions of self-mating on mating success directly carry over to the present situation.

However, the correspondence $R_i^c = \frac{1}{2}(R_{Fi}^c + R_{Mi}^c)$ also sheds light on an important difference between the two levels of mating. Considering the frequencies $P(T_i \times T_i)$ of homotypic matings and subtracting equation (5.11) from equation (5.5), the first of which refers to matings on the level of gametes and the second to matings on the level of the individual, one obtains $\frac{1}{4}(R_{Fi}^c - R_{Mi}^c)^2(1 - P^s)$ when applying the above correspondence between the cross-mating references. Thus, on both levels the mating frequencies are identical if and only if the male and female cross-mating references are identical. If they are not, the frequencies of homotypic matings on the level of the individual always exceed those on the level of gametes. This result can be restated in an intuitively more appealing form when applying the previously introduced notion of "sexual asymmetry" to the situation where female and male mating references differ from each other:

Result

In cosexual populations with random cross-mating (cross-fertilization) on the level of the gametes, the frequency of homotypic matings decreases with increasing sexual asymmetry of the cross-mating references, provided the types involved do not practice complete self-mating.

This is, of course, only meaningful for a situation in which the proportions P_i^s of self-mating and the sums $R_{Fi}^c + R_{Mi}^c$ of the sexual-specific cross-mating references do not change. The above-described effect of sexual asymmetry should thus be interpreted only within this frame of conditions.

Sexual asymmetry of the cross-mating references finds its counterpart in the sexual-specific mating participations and self-mating proportions as well as in the functional sex. Forming the difference $P(T_{Fi}) - P(T_{Mi})$ between the sex-specific mating participations and applying the equations (5.8) in connection with (5.2) one obtains

$$P(T_{Fi}) - P(T_{Mi}) = \tfrac{1}{2}(R^c_{Fi} - R^c_{Mi}) \cdot (1 - P^s).$$

Sexual symmetry of the cross-mating references ($R^c_{Fi} = R^c_{Mi}$) is thus equivalent to sexual symmetry of the mating participations ($P(T_{Fi}) = P(T_{Mi})$). According to equation (5.2), this, in turn, implies $P^s_{Fi} = P^s_{Mi}$, so that by application of the equations (5.1) or (5.4) the functional sex is $\Phi_i = \frac{1}{2}$.

In connection with equal mating success for all types ($h_i \equiv 1$), this reveals a further important consequence of sexual symmetry. Since $R^c_{Fi} = R^c_{Mi} = R^c_i$ and $P^s_{Fi} = P^s_{Mi} = P^s_i$, it follows from the representation of the frequencies of homotypic matings preceding equation (5.5) that $P_{i \lhd i} = R^c_i(1 - P^s_i) + P^s_i$. From the identity of the mating successes, it furthermore follows that $R^c_i = Q_i(1 - P^s_i)/(1 - P^s)$ and $P(T_i) = Q_i$ (compare the statements following equation (5.6)). Combining these two facts, it can be proven* that the inequality $P_{i \lhd i} > Q_i$ holds for all i if for at least one type $P^s_i > 0$ holds. This can be stated as in the following Table.

Result

If the cross-mating references are sexually symmetric and if all types have identical mating success, then the homotypic matings are more frequent than in the corresponding product structure, i.e.

$$P(T_i \times T_i) > P(T_i)^2 \quad \textit{for all } i, \tag{5.13}$$

provided at least one type practices self-mating and all cross-matings occur at random.

For natural mating references (both for cross- and self-mating, i.e. $R_{i \lhd j} = R_i = Q_i$ and thus $P(T_i) = R_i$) equation (5.13) is equivalent to

---

[*] Since $P^s = \sum_j Q_j P^s_j \geq Q_i P^s_i$ and thus $R^c_i \geq Q_i(1 - P^s_i)/(1 - Q_i P^s_i)$ holds, one obtains $P_{i \lhd i} - Q_i \geq P^s_i - Q_i + Q_i(1 - P^s_i)^2/(1 - Q_i P^s_i) = [(P^s_i - Q_i)(1 - Q_i P^s_i) + Q_i(1 - P^s_i)^2]/(1 - Q_i P^s_i) = [P^s_i(1 - Q_i P^s_i) + Q_i(P^s_i Q_i + (P^s_i)^2 - 2P^s_i)]/(1 - Q_i P^s_i) = P^s_i(1 - 2Q_i + Q_i^2)/(1 - Q_i P^s_i) = P^s_i(1 - Q_i)^2/(1 - Q_i P^s_i) \geq 0$.

$U_{i \triangleleft i} > 1$, so that in this case positive assortative mating is realized (see section 1.2).

5.3 A model based on female self-mating proportions

In order to illustrate the preceding general considerations with the help of a concrete example, the previously introduced fertility model (section 3.1) will again be drawn upon after incorporation of the effects of self-mating as specified below:

Notations

$f_i :=$ average number of female gametes produced by a T_i-individual;

$s_{Fi} :=$ proportion of self-fertilized female gametes among all female gametes produced by T_i-individuals;

$m_i :=$ average number of male gametes produced by a T_i-individual which are available for cross-fertilization;

$\bar{f} := \sum_i f_i \cdot Q_i$;
$\bar{m} := \sum_i m_i \cdot Q_i$;
$\bar{f}_{1-s} := \sum_i (1 - s_{Fi}) \cdot f_i \cdot Q_i$, or average number of cross-fertilized female gametes per individual in the total population

This model is particularly suitable for cosexual plants, since there experimental estimations of the amount of individual self-fertilization can be obtained for the ovules but are extremely difficult if not impossible to directly estimate for the pollen.

The cross-mating references of the male gametes are now given by the proportions according to which the different types contribute to the female gametes available for cross-fertilization, i.e.

$$R^c_{Fi} = \frac{f_i \cdot (1 - s_{Fi}) \cdot Q_i}{\bar{f}_{1-s}}. \tag{5.14a}$$

In the same manner one obtains the cross-mating references of the female gametes from the contributions of the single types to the set of all male gametes available for cross-pollination and fertilization:

$$R^c_{Mi} = \frac{m_i \cdot Q_i}{\bar{m}}. \tag{5.14b}$$

Under the assumption that *all female gametes be fertilized*, the female proportions of self-mating become $P^s_{Fi} = s_{Fi}$ and $P(T_{Fi}) = \frac{1}{2} f_i Q_i / \bar{f}$, so that

$$1 - P^s = 2 \cdot \sum_i (1 - P^s_{Fi}) \cdot P(T_{Fi}) = \frac{\bar{f}_{1-s}}{\bar{f}} \ .$$

When computing the (combined) proportions P^s_i of self-mating, it has to be considered that, according to the equations (5.2) and (5.8), $P(T_{Mi}) = \frac{1}{2} R^c_{Mi}(1 - P^s) + P^s_{Fi} P(T_{Fi})$ and thus $P(T_i) = P(T_{Fi}) + P(T_{Mi}) = \frac{1}{2} R^c_{Mi}(1-P^s) + (1+P^s_{Fi}) P(T_{Fi})$ holds. Application of equation (5.2) therefore yields

$$P^s_i = \frac{2 \cdot P^s_{Fi} \cdot P(T_{Fi})}{P(T_i)} = \frac{2 \cdot s_{Fi} \cdot f_i}{(1 + s_{Fi}) \cdot f_i + m_i \cdot \bar{f}_{1-s} / \bar{m}} \ . \tag{5.15}$$

From this the mating frequencies can be computed, and, in particular, the mating success results as

$$h_i = \frac{1}{2} \cdot \frac{(1 + s_{Fi}) \cdot f_i + m_i \cdot \bar{f}_{1-s} / \bar{m}}{\bar{f}} \ . \tag{5.16}$$

The classical models for the evolution of self-fertilization as they were introduced by R.A. Fisher (1941), proceed from the assumption of identical female fertilities for all types ($f_i \equiv f$) and no variation among the amounts of pollen available for cross-pollination ($m_i \equiv m$). In this case equation (5.16) takes on the form

$$h_i = 1 + \tfrac{1}{2}(s_{Fi} - \bar{s}), \quad \text{with} \quad \bar{s} = \textstyle\sum_i s_{Fi} \cdot Q_i \ , \tag{5.17}$$

so that the type with the larger proportion of self-fertilization also is superior in reproductive (mating) success. This result dominated the concepts of the evolution of self-fertilization over a long period of time.

Taking a closer look, however, it turns out that the situation $f_i \equiv f$ and $m_i \equiv m$ implies sexual asymmetry of the cross-mating references, provided there exists variation for the amounts of self-mating (self-fertilization). This raises the question as to whether sexual symmetry of the mating references has effects on the mating success that differ from the above effects of asymmetry. According to the equations (5.14) the condition $R^c_{Fi} = R^c_{Mi}$ is equivalent to $m_i = f_i(1 - s_{Fi})(\bar{m}/\bar{f}_{1-s})$, i.e. the number of male gametes of a type available for cross-matings is proportional to its number of female gametes available for cross-fertilization. Consequently, applying equation (5.16), the mating success becomes $h_i = f_i/\bar{f}$, which is no longer dependent upon the proportions of self-mating but solely depends on the female fertilities. Moreover, the consequences for sexual-specific mating participation and self-mating proportions as well as functional sexes derived at the end of section 5.2 carry over to the present situation. Thus, in this model sexual symmetry eliminates any influence of differential proportions of self-mating on mating success, which shows that Fisher's result is basically due to the sexual asymmetry inherent in the assumption of $m_i \equiv m$.

6. Genetic aspects of self-mating

From a genetic point of view, two directions of inquiry are important. The one has to do with the evolution of self-mating and thus with the conditions under which higher or lower proportions of self-mating can be evolutionarily successful or under which stable self-mating polymorphisms can occur. In many cases this requires that differences in the proportions of self-mating be correlated with differences in reproductive success (compare also the remarks in the introduction to chapter 4 on the role of the mode of inheritance).

The second direction of inquiry centers on the effects of self-mating on the structure of genotypic frequency distributions at the zygotic stage. In order to be able to discriminate between such effects and those emanating from differential reproductive success, it has to be stipulated that all genotypes have identical mating success. This stipulation is indispensable, since differences in reproductive success may as well originate from forces that show virtually no relationship to self-mating and which may therefore completely obscure the effects that are characteristic of self-mating (compare, as an example, the statements about sexual asymmetry at the end of section 5.3). It is, for this reason, meaningful to *require random cross-mating and sexual symmetry of the cross-mating references*. Under this direction of inquiry, the models treated in section 5.2 together with the above restrictions are therefore of primary concern.

The following considerations are based on a diploid gene locus with alleles A_i, $(i = 1, 2, 3, \ldots)$ and corresponding (unordered) genotypes A_iA_j. Maintaining the previous notation, these genotypes will be denoted by T_{ij}, and it will be assumed that *regular segregation is realized in the production of zygotes of each mating type*. Making use of the previously introduced “Kronecker delta” (in connection with the definition of mating frequencies in chapter 1), the frequency with which homozygotes A_iA_i can be expected to arise from matings of the type $T_{ij} \times T_{ik}$ is given by $\frac{1}{2} \cdot \frac{1}{2} + \frac{1}{2} \cdot \frac{1}{2} \cdot \delta_{ik} + \frac{1}{2} \cdot \delta_{ij} \cdot \frac{1}{2} + \frac{1}{2} \cdot \delta_{ij} \cdot \frac{1}{2} \cdot \delta_{ik} = \frac{1}{4}(1+\delta_{ij})(1+\delta_{ik})$. In a similar manner one computes the expected frequency of heterozygotes A_iA_j $(i \neq j)$ from matings of the type $T_{ik} \times T_{jl}$ as $\frac{1}{4}((1+\delta_{ik})(1+\delta_{jl}) + \delta_{jk}\delta_{il})$. These frequencies represent the **operators of inheritance**. In summary, one obtains for the expected frequencies Q'_{ij} of the genotypes A_iA_j and the expected allele frequencies $q'_i = \sum_j \frac{1}{2}(1+\delta_{ij})Q'_{ij}$ of A_i among the zygotes (and thus in the next generation):

$$\begin{aligned} Q'_{ii} &= \sum_{j\le k} P(T_{ij}\times T_{ik})\cdot\frac{1}{4}(1+\delta_{ij})(1+\delta_{ik}) \\ Q'_{ij} &= \sum_{k,l} P(T_{ik}\times T_{jl})\cdot\frac{1}{4}((1+\delta_{ik})(1+\delta_{jl})+\delta_{jk}\delta_{il}) \quad , \quad i\neq j \end{aligned} \tag{6.1a}$$

$$q'_i = \sum_j \frac{1}{2}(1+\delta_{ij})\cdot P(T_{ij}). \tag{6.1b}$$

The frequency q'_i of the allele A_i can be computed directly by considering that, under assumption of regular segregation, individuals which are heterozygous and carry the allele A_i contribute this allele only via half of their gametes to the zygote production, provided they participate in the matings. Particularly for cosexual populations, the transition equations (6.1) are fundamental for each model dealing with the change in genotypic frequencies from one generation to the next at a diploid gene locus with an arbitrary number of alleles and regular segregation. However, when applied to special models, this general formulation may in some cases turn out to be very clumsy. Its use is therefore mainly restricted to more complicated models, where a direct derivation of the transition equation is difficult, or where routine computer programs are required for computational evaluation.

Since in many cases differences in reproductive success depend on the frequencies of the genotypes, it is advisable to study the influence of self-mating on the genotypic frequencies before turning to problems of the evolution of self-mating. Moreover, the genotypic frequencies among the zygotes provide in any case the starting basis for all selective processes acting in this generation. The following treatment will therefore center upon the non-selective forces of self-mating as characterized by the above-mentioned conditions of random cross-mating, sexual symmetry of the natural cross-mating references, and absence of differential mating success.

6.1 Dynamics of genotypic frequencies

The assumptions of sexual symmetry and absence of differential mating success, which are made throughout this chapter, imply $R^c_{ij} = R^c_{Fij} = R^c_{Mij} = Q_{ij}(1-P^s_{ij})/(1-P^s)$. Together with this specification of the mating references, the mating frequencies in the equations (6.1) are then obtained with the help of the equations (5.5) or (5.11). Since the sexual-specific amounts of self-fertilization are identical, the simplifying notation $P^s_{ij} =: s_{ij}$ and $P^s =: \bar{s}$ will be used in the following, so that, in particular $\bar{s} = \sum_{i \le j} s_{ij} Q_{ij}$. Moreover, considering the frequency $q_i := \sum_j \frac{1}{2}(1 + \delta_{ij}) Q_{ij}$ of the allele A_i, the **allelic proportion of self-mating** of this allele is given by $\bar{s}_i := \sum_j \frac{1}{2}(1 + \delta_{ij}) Q_{ij} s_{ij} / q_i$; from this $\bar{s} = \sum_i \bar{s}_i \cdot q_i$.

According to equation (6.1), the allele frequencies are the same in the parental and offspring (zygote) generation, i.e. $q_i' = q_i$, since $P(T_{ij}) = Q_{ij}$ under the present assumptions. This is, in any case, a generally valid consequence of regular segregation and $h \equiv 1$.

The genotypic frequencies Q'_{ij} among the zygotes giving rise to the next generation can now be computed by applying the above-stated cross-mating references in connection with the equations (5.5) to the transition equations (6.1). However, as was pointed out earlier, it is in some cases less laborious to derive the transition equations directly rather than to carry out each single substitution in the equations (6.1). In particular, this is true for the present case, since all one has to keep in mind is that, for example, homozygotes A_iA_i among the zygotes may result either from self-matings of A_iA_i-parents (with frequency $s_{ii}Q_{ii}$) and A_iA_j-parents (with frequency $\frac{1}{4}s_{ij}Q_{ij}$) or from random cross-mating. Hence, A_iA_i-zygotes result from self-matings with frequency $s_{ii}Q_{ii} + \frac{1}{4}\sum_{j, j \neq i} s_{ij}Q_{ij} = \frac{1}{2}s_{ii}Q_{ii} + \frac{1}{2}\bar{s}_i q_i$. On the other hand, sexual symmetry among the cross-matings implies that among male as well as female gametes the allele A_i is available for cross-matings with frequency $(1 - \bar{s}_i)q_i$. Therefore, A_iA_i-zygotes result from cross-matings with frequency $(1-\bar{s}_i)q_i \cdot (1-\bar{s}_i)q_i/(1-\bar{s})$. The frequencies of heterozygotes among the zygotes can be computed in the same fashion. One thus obtains in summary:

$$\begin{aligned} Q'_{ii} &= \frac{1}{2}(s_{ii}Q_{ii} + \bar{s}_i q_i) + \frac{(1-\bar{s}_i)^2}{1-\bar{s}} \cdot q_i^2 \quad , \\ \text{for } i \neq j: \quad Q'_{ij} &= \frac{1}{2}s_{ij}Q_{ij} + \frac{(1-\bar{s}_i)(1-\bar{s}_j)}{1-\bar{s}} \cdot 2q_iq_j \quad . \end{aligned} \tag{6.2}$$

Of course, these transition equations only make sense if $\bar{s} < 1$, i.e. if not all zygotes in the population are produced by self-mating.

The frequencies Q'_{ij} can be conceived of as frequencies of matings between the alleles A_i and A_j, where all alleles have the same mating reference and show no variation in mating success. This conception defines a mating system on the level of the gametes (haplophase), the types of which are specified by the alleles they carry at the A-locus; sex does not enter into this typification. Hence, the question arises as to whether in this system the homotypic matings (with frequencies Q'_{ii}) mirror the tendency that was shown to be characteristic of the underlying mating system based on the diplophase (see equation (5.13)). In other words, the question is whether $Q'_{ii} > q_i^2$ holds. The answer can be obtained by forming the partial derivatives of Q'_{ii} in equation (6.2) with respect to the single proportions of self-mating. It turns out that all of these derivatives* are greater than or equal to 0, which proves Q'_{ii} to be an increasing function of all s-values. The desired result then follows from the fact that for $s_{kl} \equiv 0$ the identity $Q'_{ii} = q_i^2$ always holds. However, in certain cases it may occur that $Q'_{ii} = q_i^2$, even though some genotypes show positive proportions of self-mating. Consider, for example, the case of two alleles with $q_1 = q_2 = \frac{1}{2}$, $s_{11} = s_{22} = 0$ and $s_{12} > 0$. One recognizes immediately that in this situation $Q'_{11} = Q'_{22} = \frac{1}{4}$ and $Q'_{12} = \frac{1}{2}$, i.e. $Q'_{ii} = q_i^2$ for $i = 1, 2$ and $Q'_{12} = 2q_1q_2$.

Hence, under somewhat more restricted conditions, positive assortative mating as a consequence of self-mating at the level of the (diploid) genotypes (cf. the remark at the end of section 5.2) is carried over to the level of the (haploid) alleles:

Result

For random and sexually symmetric cross-mating at a diploid gene locus, the frequency of each homozygous genotype among the zygotes exceeds the square of the pertinent allele frequency, i.e.

$$Q'_{ii} > q_i^2 \quad \textit{for all } i, \tag{6.3}$$

provided all genotypes have equal mating success, regular segregation prevails, and at least one of the homozygous genotypes shows a positive proportion of self-mating.

---

* $\partial Q'_{ii}/\partial s_{ii} = Q_{ii}[1-\bar{s}-(1-\bar{s}_i)q_i]^2/(1-\bar{s})^2 > 0$; for $i \neq j$: $\partial Q'_{ii}/\partial s_{ij} = Q_{ij}[\frac{1}{2}(1-\bar{s}) - (1-\bar{s}_i)q_i]^2/(1-\bar{s})^2 \geq 0$; for $k \neq i \neq l$: $\partial Q'_{ii}/\partial s_{kl} = Q_{kl}(1-\bar{s}_i)^2 q_i^2/(1-\bar{s})^2 > 0$.

Each homozygous genotype is thus more frequent than in the corresponding product structure, so that at least one of the heterozygous genotypes must necessarily be less frequent than in the corresponding product structure, i.e $Q'_{ij} < 2q_iq_j$. However, if more than two alleles exist in the population, this need not be realized for all heterozygous genotypes.

The dynamics of the genotypic frequencies over the generations will now be demonstrated with the help of some particular cases. These cases will all be based on separated generations, and the assumption will be maintained that no selective forces other than those considered above are active. The transition equations (6.2) are therefore valid for all generations.

6.2 Complete self-mating

Suppose that all individuals carrying the homozygous genotype A_iA_i practice complete individual self-mating so that $s_{ii} = 1$. Then equation (6.2) attains the form $Q'_{ii} = Q_{ii} + \frac{1}{4}\sum_{j,j\neq i} s_{ij}Q_{ij} + (1-\bar{s}_i)^2q_i^2/(1-\bar{s})$. Consequently, as long as there exist individuals in the population which are heterozygous for the allele A_i (i.e $Q_{ij} > 0$ for at least one j with $j \neq i$), one obtains $Q'_{ii} > Q_{ii}$. Hence, in the course of the generations all genotypes heterozygous for the allele A_i must gradually disappear:

Result

If, in the present model, a homozygous genotype A_iA_i practices complete self-mating ($s_{ii} = 1$), then, after a sufficient number of generations, the allele A_i is present only in this homozygote. Hence, at equilibrium, the frequencies of the genotypes carrying the allele A_i are

$$\hat{Q}_{ii} = q_i \quad \textit{and} \quad \hat{Q}_{ij} = 0 \quad \textit{for each } j \textit{ with } j \neq i.$$

If the assumption of complete individual self-mating is extended to all homozygous individuals in the population, then, irrespective of their amounts of self-mating, heterozygotes cannot be maintained in this population indefinitely. The evolutionary process associated with these dynamics would thus lead to reproductively isolated subpopulations, each of which is characterized by complete individual self-mating and is genetically fixed at the locus considered. As a long-term consequence, large proportions of self-mating, even when restricted only to the homozygotes at a single locus, could favour genetic differentiation between subpopulations at several loci, which, in turn, is a prerequisite for speciation.

6.3 Absence of differential proportions of self-mating

The situation $s_{ij} \equiv s$ is particularly relevant for those gene loci which either have no effect on the determination of self-mating or do at least not give rise to differential proportions of self-mating. It is very likely that this applies to the vast majority of gene loci. The transition equations (6.2) now read:

$$\begin{aligned} Q'_{ii} &= \frac{1}{2}s \cdot (Q_{ii} + q_i) + (1-s) \cdot q_i^2 \\ \text{for } i \neq j\text{:} \quad Q'_{ij} &= \frac{1}{2}s \cdot Q_{ij} + (1-s) \cdot 2q_iq_j \ , \end{aligned} \tag{6.4a}$$

and the frequencies at equilibrium are in this case

$$\begin{aligned} \hat{Q}_{ii} &= q_i^2 + q_i(1-q_i) \cdot \frac{\frac{1}{2}s}{1-\frac{1}{2}s} \\ \text{for } i \neq j\text{:} \quad \hat{Q}_{ij} &= 2q_iq_j \cdot \frac{1-s}{1-\frac{1}{2}s} \ . \end{aligned} \tag{6.4b}$$

Taking advantage of these equilibrium frequencies, rearrangement of the equations (6.4a) immediately yields

$$Q'_{ij} - \hat{Q}_{ij} = \frac{1}{2}s \cdot (Q_{ij} - \hat{Q}_{ij})$$

for all i and j. Hence, over the generations, the genotypic frequencies converge to the equilibrium frequencies stated in equations (6.4b) in such a way that, in each generation, the distance from the equilibrium is reduced by a factor $\frac{1}{2}s$. Even for complete self-mating ($s = 1$), this convergence proceeds very fast, since the deviation from the equilibrium is halved in each generation for each genotype. Therefore, the relationships between genotypic and allelic frequencies as described by equation (6.4b) can be considered to be characteristic of the situation of uniformly distributed proportions of self-mating (see also Karlin 1969 p.12). As was previously the case, again $Q_{ii} > q_i^2$. In addition to this, the inequality $Q_{ij} < 2q_iq_j$ holds now for *all* heterozygotes irrespective of the number of alleles at the gene locus. Recall that this need not be realized if the population is not at equilibrium.

Restatement of this result in terms of mating preferences as applied to the alleles yields: each allele shows a positive preference for its own type and a negative preference for all other types. This statement can be made even more precise by explicit formulation of the mating preferences of the alleles, which, for short, will be termed **allele preferences (def)**. In the present context, $U_{i\triangleleft j}$ denotes the preference of the allele A_j for the allele A_i, the natural mating references are $R_{i\triangleleft j} = q_i$, and the mating frequencies are $P(A_i \times A_j) = Q'_{ij}$. Hence, $P(A_i) = q_i = R_{i\triangleleft j}$, and one obtains for the equilibrium frequencies ($Q'_{ij} = Q_{ij} = \hat{Q}_{ij}$, see equation (6.4b)):

$$\hat{U}_{i\triangleleft i} = 1 + \frac{1-q_i}{q_i} \cdot \frac{\frac{1}{2}s}{1-\frac{1}{2}s} \; , \quad \hat{U}_{i\triangleleft j} = \frac{1-s}{1-\frac{1}{2}s} \quad \text{for } i \neq j.$$

As the most conspicuous feature of these preferences one observes that all heterotypic allele preferences are identical and depend solely upon the proportion of self-mating. With increasing values for s these preferences decrease. On the other hand, the homotypic allele preferences additionally depend upon the frequency of the respective allele, and they increase with increasing s. Moreover, for a given value of s the preference of an allele for its own type is negatively frequency dependent (increases with decreasing allele frequency). This dependence is very strong, and it can lead to extremely large self-preferences for small frequency of this allele, provided the proportion of self-mating does not decrease proportionally. For example, if $q_i \leq \frac{1}{2}s$, the self-preference of the allele A_i at equilibrium is at least twice as large as the average preference, i.e. $\hat{U}_{i\triangleleft i} \geq 2$. Since the detection and estimation of self-fertilization plays an important role in experimental plant population genetics, these results will be briefly summarized in the following Table.

Result

For uniformly distributed proportions of self-mating and in the absence of other selective forces at a single, multiallelic gene locus, one observes the following characteristics for the allele preferences at genetic equilibrium:

- *(a) All heterotypic allele preferences are identical, less than 1 and depend solely upon the proportion of self-mating; these preferences are therefore suitable for the estimation of the proportion of self-mating.*
- *(b) The homotypic allele preferences additionally depend negatively upon the respective allele frequency and may attain very large values for a small such frequency.*

Even though self-mating implies positive assortative mating, both these systems of mating may have markedly different genetic consequences. The main reason for this is to be found in the fact that individual self-mating refers to a genealogically defined trait, while the term positive assortative mating applies to practically all traits. Genealogical traits may show differential expressions in relation to single loci (such as genetically varying proportions of self-mating), but, on the average, they affect all loci as became evident in the last section. As opposed to this, when positive assortative mating is considered for a phenotypic trait (such as body size, flower colour, timing of sexual maturity, etc.), it directly affects only those gene loci which participate in the control of this trait. Even if all of the genotypes concerned would show the same degree of positive assortative mating (which would be analogous to the present assumption of uniformly distributed proportions of self-mating) and genetic equilibrium were attained, the genotypic frequencies at other gene loci might very well be in disagreement with the expectations of positive assortive mating (e.g. $Q'_{ii} \leq q_i^2$).

7. Models of assortative mating

It was emphasized in section 2.5 that assortative mating cannot be recognized by separate consideration of a single type but rather by comparison with the pattern of mating preferences of other types. In addition, these patterns are comparable only if the types in question have identical mating references. The latter becomes especially evident when considering dioecious populations, since females and males have different mating references from the outset, and their mating behaviour is therefore comparable only within a specific context. In general, the sexual type of an individual sets “natural” limits to the composition of its potential mating partners, so that, in many cases, only types belonging to the same sex are comparable in the above sense.

Other traits, such as the timing of sexual maturity, may be considered to set similar natural limits to the opportunities for mating between individuals simply because their periods of maturity do not overlap. However, the timing as well as the period of sexual maturity may depend on many factors, including environmental components, so that even in cases of pronounced **dichogamy** (male and female sex organs are active at different times) self-fertilization may not be completely inhibited because of spontaneous overlap of flowering periods. Such traits may thus not be suitable for an exclusive characterization of the potential mating partners of an individual or type. However, it may not even be desirable to look for exclusive characterizations prior to observations of the actual matings, since in many cases the stipulation of equal mating references for all types of the same sex is a necessary prerequisite for the detection of the specific features of a mating system. This principle of analysis of mating sytems was accounted for by the introduction of “natural mating references”, and it will be maintained for the following formulation of models of assortative mating.

Dichogamy is an important source for assortative mating. The term dichogamy can be applied to different situations, including differential timing for maturation of female and male gametes in the same flower (for hermaphroditic plants), in different flowers of the same individual (monoecy) or even in different individuals (dioecy). However, for the characterization of a mating system, the essential information consists in the fact that female and male gametes can be produced (or are made available for fertilization) by individuals at different times, so that matings between certain individuals may be inhibited to some degree. Such effects may, of course, also be realized in the absence of dichogamy: in a hermaphroditic plant, for example, the male and female organs in each flower are active at the same time, but the flowers as a whole reach their states of maturity at different times. In the following the term **asynchrony of sexual maturity** will be used to generally address all forms of differential timing in sexual maturity. The absence of such differences, then termed **synchrony of sexual maturity**, describes the situation where the timing of female and male maturity is the same for all members of the population.

While asynchrony of sexual maturity more or less compels assortative mating, synchrony of sexual maturity may allow for assortative mating, for example, by behavioural differences among animals or selectivity of the pollination vectors of plants. The forms of assortative mating with synchrony of sexual maturity are manifold. Yet, there are fundamental differences as compared with asynchrony of sexual maturity, as will be demonstrated by the following two categories of models.

7.1 Asynchrony of sexual maturity

In order to enable a model formulation that can be applied to different systems of sexuality, the typification will again be chosen to include the two possible sex functions of an individual. Depending on the level (diplophase, haplophase) at which the typification is made and mating is defined, this allows for the treatment of both dioecious and cosexual populations (see chapter 3).

Consider a decomposition of the reproductive cycle of a population into disjoint time intervals such that individuals which are sexually mature in different intervals are not capable of mating with each other. In many cases such decompositions can be realized only approximately, since each individual may show arbitrary overlaps in its periods of male and/or female sexual maturity with any other. However, when mating is defined by the fusion of gametes, it is generally possible to specify disjoint time intervals satisfying the above requirement by referring the time of sexual maturity to the gametes produced and available for fertilization. With this general concept of sexual maturity, the following parametrization is applicable to a wide range of situations, where, for convenience only, the term ‘time’ is used in place of ‘time interval’, and time is denoted by t ($t = 1, 2, 3, \ldots$).

Notations

$\mu^F_{t\lhd i}$:= proportion of individuals which are sexually mature at time t among all T_{Fi}-individuals reaching sexual maturity; $\sum_t \mu^F_{t\lhd i} = 1$.

$\mu^M_{t\lhd j}$:= proportion of individuals which are sexually mature at time t among all T_{Mj}-individuals reaching sexual maturity; $\sum_t \mu^M_{t\lhd j} = 1$.

Q^F_i, Q^M_j := relative frequency of T_{Fi}- and T_{Mj}-individuals among all female and male members, respectively, of the population; $\sum_i Q^F_i = \sum_j Q^M_j = 1$.

μ^F_t := $\sum_i \mu^F_{t\lhd i} \cdot Q^F_i$ or proportion of individuals which are sexually mature at time t among all female individuals reaching sexual maturity; $\sum_t \mu^F_t = 1$.

μ^M_t := $\sum_j \mu^M_{t\lhd j} \cdot Q^M_j$ or proportion of individuals which are sexually mature at time t among all male individuals reaching sexual maturity; $\sum_t \mu^M_t = 1$.

π_t := proportion of matings taking place at time t among all matings in the population; $\sum_t \pi_t = 1$.

In order to exclude effects on the mating system that are not exclusively due to asynchrony of sexual maturity, the following additional assumptions are necessary:

- ▷ At each time t, random mating among all sexually mature types takes place.
- ▷ The proportion of individuals of a given type among all individuals reaching sexual maturity is equal to the relative frequency of this type in the population.

The first assumption is obvious, and the second assumption guarantees that all types of one sex have the same chance to reach sexual maturity. The types may differ solely with respect to the time at which they are available for mating but not with respect to their overall contribution to the pool of individuals reaching sexual maturity, since otherwise this would *a priori* introduce differential reproductive success. With these prerequisites the above parametrization is sufficient for a complete specification of the mating system, since it reflects the distribution of sexual maturity of each female and male type T_{Fi} and T_{Mj} as well as the matings actually taking place over time. Moreover, it should be kept in mind that these distributions can be referred equally well to individuals of the diplo- or the haplophase. As far as plants are concerned, the distributions of sexual maturity will mainly be specified by the timing of ovule receptivity and pollen shedding.

Computation of the mating frequencies and preferences: At time t the proportion of T_{Fi}-individuals among all sexually mature female individuals is $Q_i^F \mu_{t\lhd i}^F / \mu_t^F$, and the proportion of T_{Mj}-individuals among all sexually mature male individuals is $Q_j^M \mu_{t\lhd j}^M / \mu_t^M$. Clearly, these frequencies form the natural mating references at time t, so that random mating yields a frequency of $(Q_i^F \mu_{t\lhd i}^F / \mu_t^F) \cdot (Q_j^M \mu_{t\lhd j}^M / \mu_t^M)$ for the mating type $T_{Fi} \times T_{Mj}$ among all matings performed at this time. Moreover, among all matings performed in the population, a proportion π_t takes place at time t, so that the mating frequencies taken over the whole reproductive cycle attain the representation

$$\begin{aligned} P(T_{Fi} \times T_{Mj}) &= \sum_t \frac{Q_i^F \cdot \mu_{t\lhd i}^F}{\mu_t^F} \cdot \frac{Q_j^M \cdot \mu_{t\lhd j}^M}{\mu_t^M} \cdot \pi_t \\ &= Q_i^F \cdot Q_j^M \cdot \sum_t \frac{\mu_{t\lhd i}^F \cdot \mu_{t\lhd j}^M}{\mu_t^F \cdot \mu_t^M} \cdot \pi_t \, , \end{aligned} \tag{7.1a}$$

$$\begin{aligned} P(T_{Fi}) &= \frac{1}{2} Q_i^F \cdot \sum_t \frac{\mu_{t\lhd i}^F}{\mu_t^F} \cdot \pi_t \, , \\ P(T_{Mj}) &= \frac{1}{2} Q_j^M \cdot \sum_t \frac{\mu_{t\lhd j}^M}{\mu_t^M} \cdot \pi_t \, . \end{aligned} \tag{7.1b}$$

The natural mating references for the total reproductive cycle are now $R_{Fi\lhd Mj} = Q_i^F$ and $R_{Mj\lhd Fi} = Q_j^M$, so that, for this period, one arrives at the mating preferences

$$U_{Fi\lhd Mj} = \frac{\displaystyle\sum_t \frac{\mu_{t\lhd i}^F \cdot \mu_{t\lhd j}^M}{\mu_t^F \cdot \mu_t^M} \cdot \pi_t}{\displaystyle\sum_t \frac{\mu_{t\lhd j}^M}{\mu_t^M} \cdot \pi_t} \, , \tag{7.2a}$$

$$U_{Mj\triangleleft Fi} = \frac{\displaystyle\sum_t \frac{\mu^F_{t\triangleleft i}\cdot\mu^M_{t\triangleleft j}}{\mu^F_t\cdot\mu^M_t}\cdot\pi_t}{\displaystyle\sum_t \frac{\mu^F_{t\triangleleft i}}{\mu^F_t}\cdot\pi_t}\ . \tag{7.2b}$$

If, in particular, all types of one sex, the male say, do not differ with respect to their distributions of sexual maturity over time, i.e. $\mu^M_{t\triangleleft j}=\mu^M_t$ for all j, then the mating preferences become $U_{Fi\triangleleft Mj}=\sum_t \pi_t\mu^F_{t\triangleleft i}/\mu^F_t$ and $U_{Mj\triangleleft Fi}=1$. Hence, in this case, all male types share the same pattern of mating preferences, and the female types mate at random. Consequently, sexual selection in the female sex rather than assortative mating takes place.

Result

In the present model of asynchrony of sexual maturity, assortative mating can be realized only if within each of the two sexes the types differ with respect to their distributions of sexual maturity over time. If only one of the sexes show such differences, then the other mates at random and is thus sexually selected.

Specification of the π_t's: So far, no assumptions as to the laws shaping the proportions π_t were made. In fact, the model assumptions considered until now include no explicit instructions on the computation of the π_t's, since the mode according to which individuals which are sexually mature at the same time participate in the mating process was not specified. There are many such modes, among which only two will be considered in more detail.

If at each time a sufficiently large number of sexually mature male individuals is available, all sexually mature female individuals may mate. For dioecious animal populations, this would require polygyny, in case there are less males than females. As applied to plants, a sufficiently large pollen production must be realized, so that, in connection with the available pollination vectors, all ovules can be fertilized. It is characteristic of any of these situations that the female is exceeded by the male reproductive potential, which, in turn, implies competition within the male sex for mating with the females. In any case, if all sexually mature female individuals mate or have at least the same probability of mating, then the total number of matings performed at each time is determined by the females, which thus implies $\pi_t = \mu_t^F$. Under this assumption, the mating frequencies given in equation (7.1) attain the form

$$\begin{aligned} P(T_{Fi} \times T_{Mj}) &= Q_i^F \cdot Q_j^M \cdot \sum_t \frac{\mu_{t \lhd i}^F \cdot \mu_{t \lhd j}^M}{\mu_t^M} \ , \\ P(T_{Fi}) &= \frac{1}{2} Q_i^F \ , \\ P(T_{Mj}) &= \frac{1}{2} Q_j^M \cdot \sum_t \mu_{t \lhd j}^M \cdot \frac{\mu_t^F}{\mu_t^M} \ , \end{aligned} \tag{7.3}$$

and, according to equation (7.2), the mating preferences are given by

$$\begin{aligned} U_{Fi \lhd Mj} &= \frac{\sum_t \mu_{t \lhd i}^F \cdot \mu_{t \lhd j}^M / \mu_t^M}{\sum_t \mu_{t \lhd j}^M \cdot \mu_t^F / \mu_t^M} \ , \\ U_{Mj \lhd Fi} &= \sum_t \mu_{t \lhd i}^F \cdot \mu_{t \lhd j}^M / \mu_t^M \ . \end{aligned} \tag{7.4}$$

Since by equation (7.3) $P(T_{Fi})/Q_i^F = \frac{1}{2}$, *the assumption* $\pi_t = \mu_t^F$ *implies that all female types have the same mating success.*

The π_t's may also depend on both the μ_t^F's and the μ_t^M's. This may be a realistic assumption in plant populations, where at particular times the amount of pollen produced does not suffice to pollinate all female flowers. However, the mode according to which the π_t's depend on the μ_t^F's and μ_t^M's may be very complicated and need not even be proportional to the products $\mu_t^F \cdot \mu_t^M$, as one might expect intuitively. It appears that there is no common denominator to the multitude of possiblities to include both sex-specific distributions into the π_t's. Since the purpose is to give prominence to more generally applicable principles rather than to the analysis of highly specific models, such modes of dependence will not be pursued further here.

Positive and negative assortative mating

An analysis of the present model with respect to these special forms of assortative mating requires the consideration of traits that are equally expressed in both sexes. This is unnecessary for cosexual populations, since there both gametic sexes can be generated by the same individual. Moreover, in order to be able to treat cosexual and dioecious populations jointly, a 1:1 sex ratio is stipulated whenever dioecious populations are referred to, i.e. $Q_i^F = Q_i^M = Q_i$ for all i. The equations (7.1) and (7.2) should thus be viewed under these restrictions.

The fact that all types appear in both sexes allows characterization of the mating system even of a dioecious population without consideration of the sexual type of the individuals. This is also in accordance with the desire to treat cosexual and dioecious populations jointly. The mating frequencies for this situation result from the application of the equations (7.1) to the equations (3.2):

$$\begin{aligned} P(T_i \times T_j) &= Q_i \cdot Q_j \cdot \sum_t \frac{\mu_{t\triangleleft i}^F \cdot \mu_{t\triangleleft j}^M + \mu_{t\triangleleft j}^F \cdot \mu_{t\triangleleft i}^M}{\mu_t^F \cdot \mu_t^M} \cdot \pi_t \quad \text{for } i \neq j, \\ P(T_i \times T_i) &= Q_i^2 \cdot \sum_t \frac{\mu_{t\triangleleft i}^F \cdot \mu_{t\triangleleft i}^M}{\mu_t^F \cdot \mu_t^M} \cdot \pi_t \,, \end{aligned} \tag{7.5a}$$

$$P(T_i) = Q_i \cdot \sum_t \frac{1}{2} \left(\frac{\mu_{t\triangleleft i}^F}{\mu_t^F} + \frac{\mu_{t\triangleleft i}^M}{\mu_t^M} \right) \cdot \pi_t \,. \tag{7.5b}$$

The natural mating references pertaining to this situation are $R_{j\triangleleft i} = Q_j$, so that the mating preferences are given by

$$U_{j\triangleleft i} = \frac{\displaystyle\sum_t \frac{\mu_{t\triangleleft i}^F \cdot \mu_{t\triangleleft j}^M + \mu_{t\triangleleft j}^F \cdot \mu_{t\triangleleft i}^M}{\mu_t^F \cdot \mu_t^M} \cdot \pi_t}{\displaystyle\sum_t \left(\frac{\mu_{t\triangleleft i}^F}{\mu_t^F} + \frac{\mu_{t\triangleleft i}^M}{\mu_t^M} \right) \cdot \pi_t} \quad \text{for } i \neq j, \tag{7.6a}$$

$$U_{i\triangleleft i} = \frac{\displaystyle\sum_t \frac{\mu_{t\triangleleft i}^F \cdot \mu_{t\triangleleft i}^M}{\mu_t^F \cdot \mu_t^M} \cdot \pi_t}{\displaystyle\sum_t \frac{1}{2} \left(\frac{\mu_{t\triangleleft i}^F}{\mu_t^F} + \frac{\mu_{t\triangleleft i}^M}{\mu_t^M} \right) \cdot \pi_t} \,. \tag{7.6b}$$

The mating success of all males and females of type T_i is by definition $h_i = P(T_i)/Q_i$, which yields after substitution into the last of the equations (7.5)

$$h_i = \sum_t \frac{1}{2}\left(\frac{\mu^F_{t\lhd i}}{\mu^F_t} + \frac{\mu^M_{t\lhd i}}{\mu^M_t}\right)\cdot \pi_t \ . \tag{7.7}$$

The extreme form of negative assortative mating of a type T_i is of course realized, if both sexes of this type are never simultaneously sexually mature, i.e. if $\mu^F_{t\lhd i}\cdot\mu^M_{t\lhd i} = 0$ for all t and thus $U_{i\lhd i} = 0$. Such a type is usually said to practice **completely negative assortative mating**. The opposite extreme form is then **completely positive assortative mating**, and it characterizes the situation where a type T_i does not mate with types other than its own, which implies for the present model $\mu^F_{t\lhd i}\cdot\mu^M_{t\lhd j} = \mu^F_{t\lhd j}\cdot\mu^M_{t\lhd i} = 0$ for all t and all j with $j \neq i$. In this case $U_{j\lhd i} = 0$ for all j with $j \neq i$. Since the present models allow for the realization of these extreme forms, intermediate forms of assortative mating can also occur.

In particular, if the types within one sex, the male say, do not differ with respect to their distributions of sexual maturity over time, i.e. $\mu^M_{t\lhd i} = \mu^M_t$ for all t and i, then random mating prevails, irrespective of the distribution in time of sexual maturity of the other sex (the female), provided at each time the proportion of matings taking place is equal to the proportion of sexually mature individuals in this other sex (the female), i.e. provided $\pi_t = \mu^F_t$ for all t. Random mating, in turn, implies equal mating success for all types (see section 2.1). The latter, however, may also be realized if random mating does not take place.

If for each type its distribution in time of female and male sexual maturity is the same (**sexual symmetry**), i.e. $\mu^F_{t\lhd i} = \mu^M_{t\lhd i} = \mu_{t\lhd i}$ for all t and i, then also $\mu^F_t = \mu^M_t = \mu_t$. If, in addition, $\pi_t = \mu_t$, one obtains, by using equation (7.7), $h_i = 1$ for all i, so that all types have the same mating success. Furthermore, it can be shown* that, for this situation, $U_{i\lhd i} \geq 1$ for all i, where $U_{i\lhd i} = 1$ only for those types T_i having the same distribution of sexual maturity in time as that realized in the total population, i.e. $\mu_{t\lhd i} = \mu_t$ for all t. Hence, $U_{i\lhd i} < 1$ requires sexual asymmetry for at least one type in case $\pi_t = \mu^F_t$ for all t. This is summarized in the following Table.

---

* From the inequality between the arithmetic and harmonic mean it follows that $\left(\sum_t \mu_{t\lhd i}\cdot(\mu_{t\lhd i}/\mu_t)\right)^{-1} \leq \sum_t \mu_{t\lhd i}\cdot(\mu_t/\mu_{t\lhd i}) = 1$, where equality occurs only if $\mu_{t\lhd i} = \mu_t$ for all t. Hence, $U_{i\lhd i} = \sum_t(\mu_{t\lhd i})^2/\mu_t \geq 1$.

Result

Basically, asynchrony of sexual maturity does not exclude random mating, as can be concluded from the example of identical distributions of sexual maturity for all types in the male sex only, combined with $\pi_t = \mu_t^F$ *for all* t*.*

The assumption that $\pi_t = \mu_t^F$ *for all* t *has the following consequences: Sexual symmetry for all types implies that all these types have the same mating success and mate positively assortatively. Differences in the distribution of sexual maturity between the types in the male sex and sexual asymmetry are necessary prerequisites for both negative assortative mating and differential mating success.*

In the following, conditions for superiority in mating success of one type over another will be studied in more detail. For this purpose it is sufficient to restrict the above considerations to two types for which the total reproductive cycle of the population is decomposed into either two or three mutually disjoint intervals of sexual maturity.

Two types, two time intervals of sexual maturity, and $\boldsymbol{\pi_t = \mu_t^F}$**:** The difference between the mating success of two types, as it follows from equation (7.7) together with the condition $\pi_t = \mu_t^F$, can be represented more clearly if one considers the fact that now $\mu_{1\lhd 1}^M - \mu_{1\lhd 2}^M = \mu_{2\lhd 2}^M - \mu_{2\lhd 1}^M$, $\mu_2^F = 1 - \mu_1^F$, and $\mu_2^M = 1 - \mu_1^M$ hold:

$$2 \cdot \mu_1^M \cdot \mu_2^M \cdot (h_1 - h_2) = (\mu_{t\lhd 1}^M - \mu_{t\lhd 2}^M) \cdot [Q_1(\mu_{t\lhd 1}^F - \mu_{t\lhd 1}^M) + Q_2(\mu_{t\lhd 2}^F - \mu_{t\lhd 2}^M)];$$

recall that now $t = 1$ or $t = 2$. The following results can be derived directly from this representation:

(I) If the two differences $\mu_{t\lhd 1}^F - \mu_{t\lhd 1}^M$ and $\mu_{t\lhd 2}^F - \mu_{t\lhd 2}^M$ have the same sign, then it holds that for all frequencies Q

(a) type T_1 is superior to type T_2 in mating success if the sign of $\mu_{t\lhd 1}^M - \mu_{t\lhd 2}^M$ is identical to that of the other two differences,

(b) type T_1 is inferior to type T_2 in mating success if the sign of $\mu_{t\lhd 1}^M - \mu_{t\lhd 2}^M$ is the opposite of that of the other two differences.

(II) If the two differences $\mu_{t\lhd 1}^F - \mu_{t\lhd 1}^M$ and $\mu_{t\lhd 2}^F - \mu_{t\lhd 2}^M$ have different signs, then for sufficiently low frequency of the one or other type

(a) the rare type is superior to the frequent type in mating success if the sign of $\mu_{t\lhd 1}^M - \mu_{t\lhd 2}^M$ is equal to that of $\mu_{t\lhd 2}^F - \mu_{t\lhd 2}^M$,

(b) the rare type is inferior to the frequent type in mating success if the sign of $\mu^M_{t\lhd 1} - \mu^M_{t\lhd 2}$ is equal to that of $\mu^F_{t\lhd 1} - \mu^M_{t\lhd 1}$.

In the case (II) there always exists a frequency distribution $Q = \hat{Q}$ of the types, such that both types have the same mating success, i.e. $h_1 = h_2 = 1$. This distribution is obtained by equating to 0 the expression in brackets appearing in the above equation and solving this for Q_1 ($= 1 - Q_2$):

$$\begin{aligned}\hat{Q}_1 =& \frac{\mu^M_{t\lhd 2} - \mu^F_{t\lhd 2}}{\mu^F_{t\lhd 1} + \mu^M_{t\lhd 2} - \mu^F_{t\lhd 2} - \mu^M_{t\lhd 1}}\ ,\\ \hat{Q}_2 =& 1 - \hat{Q}_1 = \frac{\mu^F_{t\lhd 1} - \mu^M_{t\lhd 1}}{\mu^F_{t\lhd 1} + \mu^M_{t\lhd 2} - \mu^F_{t\lhd 2} - \mu^M_{t\lhd 1}}\ .\end{aligned}$$

According to whether $Q_1 < \hat{Q}_1$ or $Q_1 > \hat{Q}_1$, in the case (IIa) $h_1 > h_2$ or $h_1 < h_2$, respectively, while this is reversed in the case (IIb), i.e. $h_1 < h_2$ for $Q_1 < \hat{Q}_1$ and $h_1 > h_2$ for $Q_1 > \hat{Q}_1$.

The conditions (I) and (II) can be expressed in an intuitively more appealing way if one considers the fact that, for example, $\mu^F_{t\lhd 1} - \mu^M_{t\lhd 1} > 0$ and $\mu^F_{t\lhd 2} - \mu^M_{t\lhd 2} > 0$ describes the situation where, at the same time t, both types are sexually mature to a greater proportion as female than as male. This situation can be generalized by requiring $(\mu^F_{t\lhd 1} - \mu^M_{t\lhd 1}) \cdot (\mu^F_{t\lhd 2} - \mu^M_{t\lhd 2}) > 0$ for all t, in which case the two types will be called **sexually asymmetric in the same direction**. Consequently, the two types are called **sexually asymmetric in opposite directions**, if the products of the differences are negative, i.e. where one type is sexually mature to a greater proportion as female than as male, while the opposite is true for the other type at each given instance of time. This terminology allows for a purely verbal statement of the above conditions in the following Table.

Result

If the two types are sexually asymmetric in the same direction (case (I)), then one type is always globally superior (irrespective of its frequency) in mating success to the other type. For this case, consider the time at which both types are sexually mature to a greater proportion as female than as male; then the superior type is the one which has, at this time, the greater proportion of male sexual maturity.

If the two types are sexually asymmetric in opposite directions (case (II)), then the superiority of one type over the other in mating success depends on its frequency. For this case, fix any instant of time and consider the type which has, at this time, the smaller proportion of male sexual maturity. If this type is at this time sexually mature to a larger proportion as female than as male, then, at sufficiently extreme frequencies, the rare type is superior to the frequent type in mating success. In the opposite case (if this type is at this time sexually mature to a larger proportion as male than as male), the rare type is inferior to the frequent type.

The fact that, in both kinds of sexual asymmetry, the difference between the two types in their proportions of male sexual maturity decides on the superiority in mating success is closely connected with the assumption $\pi_t = \mu_t^F$. As was previously demonstrated, this assumption implies competition among the males (pollen) but not among the females (ovules) for access to mating.

The case remaining to be considered is the one in which *the distribution of sexual maturity over time is sexually symmetric for one and sexually asymmetric for the other type.* If T_1, say, is the sexually symmetric type with $\mu_{t\lhd 1}^F = \mu_{t\lhd 1}^M = \mu_{t\lhd 1}$, the above equation for the difference in mating success between the two types reduces to $2\mu_1^M \mu_2^M (h_1 - h_2) = (\mu_{t\lhd 1} - \mu_{t\lhd 2}^M)(\mu_{t\lhd 2}^F - \mu_{t\lhd 2}^M) Q_2$. Hence, according to whether the right side of the last equation is positive or negative, T_1 or T_2 is superior in mating success. The superiority does not depend on the frequencies of the types in the population and is thus global. The situation is therefore akin to that of sexual asymmetry in the same direction.

Result

Consider the instance of time at which the proportion of female sexual maturity of the sexually asymmetric type exceeds its proportion of male sexual maturity. If at this time the proportion of male sexual maturity of the symmetric type exceeds that of the asymmetric type, then the symmetric type is globally superior in mating success to the asymmetric type; the opposite holds if the proportion of male sexual maturity of the asymmetric type exceeds that of the symmetric type.

The most extreme form of sexual asymmetry is **consecutive hermaphroditism**. In terms of the proportions of sexual maturity, this is realized if, for example, $\mu^F_{1\triangleleft 2} = 1$, $\mu^M_{1\triangleleft 2} = 0$, $\mu^F_{2\triangleleft 2} = 0$ and $\mu^M_{2\triangleleft 2} = 1$, and it implies global superiority of the sexually symmetric type irrespective of its distribution of sexual maturity over time.

However, strong forms of sexual asymmetry may also be advantageous compared to sexual symmetry, provided these forms do not reach the extent of genuinely consecutive hermaphroditism and the sexual maturity of the symmetric type is concentrated on a single time interval. For example, if the symmetric type T_1 is sexually mature only at time $t = 1$ (so that $\mu_{1\triangleleft 1} = 1$, $\mu_{2\triangleleft 1} = 0$), it is inferior to the asymmetric type if the latter is at this time sexually mature in both its sexes, and if its proportion of female sexual maturity is larger than its proportion of male sexual maturity. If the asymmetry were very strong and, due to its superiority, the asymmetric type would continuously increase in frequency over the course of the generations, a peculiar situation would result. As a consequence, the population would consist almost entirely of individuals of the asymmetric type which have hardly any opportunities to mate with each other, since in one interval of the reproductive cycle almost only female and in the other almost only male individuals are sexually mature. Thus, the population would be bound for extinction.

The last example reveals a basic problem involved with the assumption $\pi_t = \mu_t$, which states that all sexually mature female individuals have the same chance to participate in the mating process. In this example the assumption $\pi_t = \mu_t$ is difficult to justify, since at one instant of time, a few female individuals have abundant male individuals to mate with, while at the other instant of time many female individuals have to share a few male individuals. The simultaneous existence of sexually symmetric and extremely asymmetric types in a population is thus likely to introduce frequency dependence for the probabilities of mating. Models considering this aspect by including effects of frequency dependent probabilities for pollination of ovules on differential mating success in plant populations were analysed in some detail by Häcker (1986).

Two types, three time intervals of sexual maturity, and $\pi_t = \mu^F_t$: A meaningful distinction from the case of two intervals of sexual maturity is obtained by the assumption that there is only one such interval within which both types are simultaneously sexually mature. For reasons of continuity in time this interval should be intermediate and should thus be the second interval ($t = 2$). In addition to the second interval, type T_1 is assumed to be sexually mature in the first but not in the third interval ($\mu^F_{3\lhd 1} = \mu^M_{3\lhd 1} = 0$), while type T_2 is additionally sexually mature in the third but not in the first interval ($\mu^F_{1\lhd 2} = \mu^M_{1\lhd 2} = 0$). This situation is illustrated in the following table, where + := sexually mature and 0 := not sexually mature:

	T_1	T_2
$t = 1$	$+$	0
$t = 2$	$+$	$+$
$t = 3$	0	$+$

Hence, at time $t = 1$ matings are possible only among indivduals of type T_1, and at time $t = 3$ matings take place only among T_2-individuals. Therefore $\mu^F_{1\lhd 1} = 1 - \mu^F_{2\lhd 1}$, $\mu^M_{1\lhd 1} = 1 - \mu^M_{2\lhd 1}$, $\mu^F_{2\lhd 2} = 1 - \mu^F_{3\lhd 2}$, $\mu^M_{2\lhd 2} = 1 - \mu^M_{3\lhd 2}$, $\mu^F_1 = \mu^F_{1\lhd 1} Q_1$, $\mu^M_1 = \mu^M_{1\lhd 1} Q_1$, $\mu^F_3 = \mu^F_{3\lhd 2} Q_2$, $\mu^M_3 = \mu^M_{3\lhd 2} Q_2$, $\mu^F_2 = \mu^F_{2\lhd 1} Q_1 + \mu^F_{2\lhd 2} Q_2$, and $\mu^M_2 = \mu^M_{2\lhd 1} Q_1 + \mu^M_{2\lhd 2} Q_2$. According to equation (7.7) it follows from this that the difference between the mating successes obey the relationship

$$2 \cdot \mu^M_2 \cdot (h_1 - h_2) = \mu^F_{2\lhd 2} \cdot \mu^M_{2\lhd 1} - \mu^M_{2\lhd 2} \cdot \mu^F_{2\lhd 1},$$

so that both types are either globally (for all frequencies) identical or one type is globally superior to the other in mating success. Identity in mating success is not restricted to sexual symmetry. The following result is thus characteristic of the present model:

Result

Type T_1 is superior to type T_2 in mating success if, at the time of simultaneous sexual maturity of both types, type T_1 has more sexually mature male individuals per sexually mature female individual than type T_2, i.e. if

$$\frac{\mu^M_{2\triangleleft 1}}{\mu^F_{2\triangleleft 1}} > \frac{\mu^M_{2\triangleleft 2}}{\mu^F_{2\triangleleft 2}}$$

Some special cases are again of interest, all of which refer to the conditions in the interval $t = 2$ of simultaneous sexual maturity of the two types. For example, if type T_1, say, is sexually symmetric and type T_2 is sexually asymmetric, then the first surpasses the second type in mating success only if at time $t = 2$ the second type is sexually mature to a greater proportion as female than as male. In the oposite case the sexually asymmetric type is superior to the symmetric type. If the proportions of female sexual maturity are the same for both types at time $t = 2$, then that type with the larger proportion of male sexual maturity is superior. For equal proportions of male sexual maturity of the two types, however, the type with the lower proportion of female sexual maturity is superior. It again turns out that the assumption $\pi_t = \mu^F_t$ entails different effects of the two sexes on the respective mating success.

7.2 Synchrony of sexual maturity

If all members of a population are sexually mature at the same time, they can, at least in principle (and taking account of the sexual system), all be potential mating partners for each other. The realization of special mating preferences will in this case mainly depend on particular propensities or predispositions of single individuals, or on factors that affect the mating process directly. Indirectly acting factors play an important role in plant populations, since, because of the immobility of the individuals, pollination vectors are required to overcome spatial distances.

In order to give a generally applicable and clear idea of the forces that may guide mating processes particularly for synchrony of sexual maturity, it is useful to introduce the term **mating predisposition** as a technical term. For example, a female may be deterred from mating with particular males by certain physiological or morphological characteristics; such a female would have a negative predisposition toward these males. Such predisposing factors may, however, also be determined by environmental conditions. Among these are, for example, differential mating behaviour under varying physical-ecological conditions, dependence of pollination between plants of particular flower colour upon the presence of particular pollinator organisms (as biotic environmental factors), or the dependence of the opportunities for fertilization upon the spatial distance between potential mating partners.

All factors that are assumed to predispose matings must enter into the typification of the individuals concerned, in order to enable a meaningful characterization of the mating system. However, predispositions for mating need not directly determine the matings which are actually performed. Predispositions for mating and their realization as measured by the (actual) mating preferences thus need not be identical. This becomes evident when considering the extreme example where a type T_1 has a positive predisposition for mating with a type T_2, but where this latter type is not present in the population; T_1-individuals thus have no chance to realize their predisposition. Moreover, the extent to which the predisposition can be realized may depend on the frequency of the preferred type. In other words, in addition to statements about mating predispositions, the (constructive) specification of a mating system requires a description of conditions that control the realization of these predispositions. As will become clear in the following models, these conditions may even cause individuals having no predispositions at all to actually mate preferentially, which contradicts the intuitive expectation of random mating for such individuals.

In a generalized sense, the sexual type and the time of sexual maturity may also be considered as factors introducing mating predispositions. Hence the composition of the potential mating partners of a given type may to a large degree be determined by the mating predispositions of this type as well as by the predispositions of the potential mating partners. Under this general premise, even the previous models of asynchrony of sexual maturity (section 7.1) and individual self-mating (chapter 5) can be conceived of as special cases of the present concept of mating predisposition. Karlin (1969, as cited in chapter 6) provides a good account of the models of assortative mating commonly used in population genetics, all of which can be subsumed under the concept of mating predisposition and many of which are special cases of the models to be treated in the following.

POSITIVE ASSORTATIVE MATING (HOMOTYPIC PREDISPOSITION)

The simplest models of positive assortative mating are probably those based on the idea that individuals have a predisposition to mate with individuals of their own type. Not all individuals are required to have this mating predisposition, but those not having it are considered in these models to have no predispositions at all (i.e. no predispositions for individuals differing from their own type). In order to avoid confusion about the term 'positive assortative mating', it is suggested that models of the above kind be termed **homotypic mating predisposition**. As was already argued, whether homotypic mating predisposition actually leads to positive assortative mating (as becomes manifest in the mating preferences U) depends on further conditions of the mating process and has, therefore, to be verified in each single case.

The following parametrization of homotypic mating predisposition is again oriented at dioecious populations. However, according to the meanwhile well-known technique of identification, it can be applied to cosexual populations as well. The typification must, of course, be applicable to both sexes, since otherwise homotypic matings would not be defined.

Notations

α_{Fi} := relative frequency of homotypically predisposed individuals among all T_{Fi}-individuals;

α_{Mi} := relative frequency of homotypically predisposed individuals among all T_{Mi}-individuals;

$\alpha_F := \sum_i \alpha_{Fi} \cdot Q_i^F$, or relative frequency of homotypically predisposed individuals among all female members of the population;

$\alpha_M := \sum_i \alpha_{Mi} \cdot Q_i^M$, or relative frequency of homotypically predisposed individuals among all male members of the population;

The set of potential mating partners of non-predisposed T_{Fi}-females consists of all non-predisposed males (with proportion $1 - \alpha_M$) plus all predisposed T_{Mi}-males (with proportion $\alpha_{Mi} \cdot Q_i^M$). Thus, among the potential mating partners of non-predisposed T_{Fi}-females, a fraction

$$R^c_{Mj \lhd Fi} = \frac{\delta_{ij} \cdot \alpha_{Mi} \cdot Q_i^M + (1 - \alpha_{Mj}) \cdot Q_j^M}{1 - \alpha_M + \alpha_{Mi} \cdot Q_i^M}$$

consists of males of type T_{Mj}. The mating references of non-predisposed males can be derived in an analogous manner as

$$R^c_{Fj \lhd Mi} = \frac{\delta_{ij} \cdot \alpha_{Fi} \cdot Q_i^F + (1 - \alpha_{Fj}) \cdot Q_j^F}{1 - \alpha_F + \alpha_{Fi} \cdot Q_i^F}.$$

The above-defined parameters of homotypic predisposition should, in general, not be considered as constant values. For example, the α's may become frequency dependent in that an individual abandons its previous predisposition if it has not encountered its own type after a certain number of mating contacts. This event will in most cases increase in likelihood with decreasing frequency of the type in the population. A possible advantage of such behaviour for an organism could be seen in the avoidance of having its mating success be impaired by its predisposition. One of the models to be presented later will provide an example for this.

Irrespective of the existing mating predispositions, the maximum number of matings possible in a dioecious population can, above all, be limited by the sex ratio in connection with the possibility of single or multiple matings. In monogamous populations, for example, the number of matings is limited by the less frequent sex, while in polygynous populations all females have the chance to mate, provided the number of females per male is not too large. In any case, the mode according to which the circumstances of mating allow the mating predispositions to influence the mating success is of central importance. It is thus advisable to basically classify the circumstances of mating with respect to whether they do or do not entail effects of the predispositions on mating success.

Independence of female mating success from mating predispositions: Under this premise $P(T_{Fi}) = \frac{1}{2} Q_i^F$ holds for all i, which is thus equivalent to identical mating success for all female types. This condition can be met by dioecious animal populations with expressed polygyny or by plant populations with abundant pollen production. Furthermore, it will be assumed that non-predisposed female types mate at random with respect to the mating references $R^c_{Mj\triangleleft Fi}$, so that the mating norms are given by

$$P_{Mj\triangleleft Fi} = \delta_{ij} \cdot \alpha_{Fi} + (1-\alpha_{Fi}) \cdot R^c_{Mj\triangleleft Fi} \ .$$

Inserting the above mating references, one obtains the mating frequencies according to equation (1.1):

$$\begin{aligned} P(T_{Fi} \times T_{Mj}) =& \delta_{ij}\alpha_{Fi}Q_i^F \\ &+ Q_i^F(1-\alpha_{Fi}) \cdot \frac{\delta_{ij}\alpha_{Mi}Q_i^M + (1-\alpha_{Mj})Q_j^M}{1-\alpha_M+\alpha_{Mi}Q_i^M}, \end{aligned} \tag{7.8a}$$

$$\begin{aligned} P(T_{Mi}) =& \frac{1}{2}\alpha_{Fi}Q_i^F + \frac{1}{2}\frac{\alpha_{Mi}(1-\alpha_{Fi})Q_i^F Q_i^M}{1-\alpha_M+\alpha_{Mi}Q_i^M} + \\ &+ \frac{1}{2}(1-\alpha_{Mi})Q_i^M \cdot \sum_j \frac{(1-\alpha_{Fj})Q_j^F}{1-\alpha_M+\alpha_{Mj}Q_j^M} \ . \end{aligned} \tag{7.8b}$$

The question of primary interest is now whether homotypic mating predisposition implies positive assortative mating in both sexes. For this purpose consider the sign of the difference $U_{Mi\triangleleft Fi} - U_{Mj\triangleleft Fi}$ for $i \neq j$, where the mating preferences are assumed to be based on the natural mating references $R_{Mj\triangleleft Fi} = Q_j^M$:

$$\begin{aligned} (U_{Mi\triangleleft Fi} - U_{Mj\triangleleft Fi}) \cdot (1-\alpha_M+\alpha_{Mi}Q_i^M) =& \\ =& \alpha_{Fi}\left(\alpha_{Mi} + \frac{1-\alpha_M}{Q_i^M}\right) + (1-\alpha_{Fi}) \\ &- (1-\alpha_{Fi})(1-\alpha_{Mj}) \\ =& \alpha_{Fi}\left(\alpha_{Mi} + \frac{1-\alpha_M}{Q_i^M}\right) + (1-\alpha_{Fi})\alpha_{Mj} \geq 0 \ . \end{aligned}$$

Here, the situation of equality to 0 can occur only if $\alpha_{Fi} = \alpha_{Mj} = 0$. Hence, $U_{Mi\triangleleft Fi} \geq U_{Mj\triangleleft Fi}$ for all j and therefore $U_{Mi\triangleleft Fi} \geq 1$. Moreover, the homotypic mating preference of a homotypically predisposed female type exceeds all of its heterotypic preferences. Random mating of a female type is possible only if neither this type nor any male type shows a mating predisposition. Hence, in particular, despite the absence of mating predispositions for a female type, this type may still practice positive assortative mating if all males are positively predisposed.

The relationship between the homotypic and heterotypic mating preferences of the male types are analysed analogously, where the natural mating references are now $R_{Fj\triangleleft Mi} = Q_j^F$:

$$\begin{aligned}
&(U_{Fi\triangleleft Mi} - U_{Fj\triangleleft Mi}) \cdot 2P(T_{Mi}) = \\
=&\alpha_{Fi} + \frac{(1-\alpha_{Fi})Q_i^M}{1-\alpha_M+\alpha_{Mi}Q_i^M} - \frac{(1-\alpha_{Fj})(1-\alpha_{Mi})Q_i^M}{1-\alpha_M+\alpha_{Mj}Q_j^M} \\
=&\alpha_{Fi} \cdot \frac{1-\alpha_M-(1-\alpha_{Mi})Q_i^M}{1-\alpha_M+\alpha_{Mi}Q_i^M} + \\
&+ Q_i^M \cdot \frac{1-\alpha_M+\alpha_{Mj}Q_j^M-(1-\alpha_{Fj})(1-\alpha_{Mi})(1-\alpha_M+\alpha_{Mi}Q_i^M)}{(1-\alpha_M+\alpha_{Mj}Q_j^M)(1-\alpha_M+\alpha_{Mi}Q_i^M)} \\
&\geq Q_i^M \cdot \frac{\alpha_{Mj}Q_j^M+\alpha_{Mi}(1-\alpha_M-(1-\alpha_{Mi})Q_i^M)}{(1-\alpha_M+\alpha_{Mj}Q_j^M)(1-\alpha_M+\alpha_{Mi}Q_i^M)} \geq 0 \ .
\end{aligned}$$

For the first estimation, it has to be considered that α_{Fi} and α_{Fj} are nonnegative. Hence, $U_{Fi\triangleleft Mi} \geq U_{Fj\triangleleft Mi}$ for all j, and equality is realized only for the case where α_{Fi}, α_{Fj}, α_{Mi}, and α_{Mj} are all equal to 0. As was the case with the female sex, the homotypic mating preference of a homotypically predisposed male type exceeds all of its heterotypic predispositions. However, as opposed to the situation in the female sex, homotypic predisposition of even a single type, male or female, suffices for the exclusion of random mating for *all* male types. The following Table summarizes this.

Result

If the circumstances of mating imply that, irrespective of their mating predispositions, all female types have the same mating success, then homotypic predisposition causes positive assortative mating in both sexes. The extent of homotypic mating preference of a homotypically predisposed type, whether male or female, exceeds all of its heterotypic preferences.

A female type can practice random mating only if neither it nor any of the male types is homotypically predisposed. On the other hand, homotypic predisposition of even a single type, male or female, suffices to enforce positive assortative mating for all male types. In particular, the absence of mating predispositions in one sex is thus not sufficient for the assumption of random mating for this sex.

The effects of homotypic mating predisposition on mating success in the male sex can be substantially modified by the sex ratio of the single types, as becomes apparent from consideration of the expression

$$\begin{aligned} h_{Mi} = \frac{1}{2Q_M}\Bigg(\alpha_{Fi}\cdot\frac{Q_i^F}{Q_i^M} + \frac{\alpha_{Mi}(1-\alpha_{Fi})Q_i^F}{1-\alpha_M+\alpha_{Mi}Q_i^M} \\ +(1-\alpha_{Mi})\sum_j\frac{(1-\alpha_{Fj})Q_j^F}{1-\alpha_M+\alpha_{Mj}Q_j^M}\Bigg)\,. \end{aligned} \tag{7.9a}$$

In this equation, for a given positive value of α_{Fi}, h_{Mi} may reach unrealistically large values, since the quotient Q_i^F/Q_i^M is not bounded from above. The mating success of T_{Mi}-males would increase drastically if they were to become rare, females of the same type were to become frequent, and if these male types were strongly homotypically predisposed. The reason for this unrealistic result can again be found in the assumption that the mating success of the female types be independent of their mating predispositions. Hence, this assumption appears to be more appropriate for populations in which *all types show a 1:1 sex ratio*, i.e. in which $Q_i^F = Q_i^M = Q_i$ holds for all i. In this case, which is also relevant for cosexual populations, one obtains for the male mating success by equation (7.9a):

$$\begin{aligned} h_{Mi} = \frac{1}{2Q_M}\Bigg(\alpha_{Fi} + \frac{\alpha_{Mi}(1-\alpha_{Fi})Q_i}{1-\alpha_M+\alpha_{Mi}Q_i} \\ +(1-\alpha_{Mi})\sum_k\frac{(1-\alpha_{Fk})Q_k}{1-\alpha_M+\alpha_{Mk}Q_k}\Bigg)\,. \end{aligned} \tag{7.9b}$$

Despite this simplifying assumption, the male mating success still depends in a very complex manner on the various parameters of mating predisposition. The consideration of a few special cases may help to give a clearer idea of the nature of this dependence. A simple case is provided by the absence of mating predispositions in the male sex, i.e. $\alpha_{Mi} = 0$ for all i. Then $(h_{Mi} - h_{Mj})2Q_M = \alpha_{Fi} - \alpha_{Fj}$, so that mating success is positively correlated with strength of homotypic mating predisposition. However, as soon as the male types are homotypically predisposed, such simple and frequency independent rankings of the types with respect to mating success no longer hold. In order to substantiate this assertion, the case of two types ($i = 1, 2$) shall now be treated in more detail.

Two types with 1:1 sex ratio and equal female mating success: For this case it has to be taken into account that $2Q_M(h_{M1}Q_1+h_{M2}Q_2)=1$. Hence, type T_1 is superior to type T_2 in mating success if and only if $2Q_Mh_{M1}>1$ holds, so that the sign of $2Q_Mh_{M1}-1$ decides on which type is superior. Applying equation (7.9b) to two types, one obtains

$$\begin{aligned}2Q_M\cdot h_{M1}-1&=\alpha_{F1}+\frac{(1-\alpha_{F1})Q_1}{1-\alpha_M+\alpha_{M1}Q_1}+\frac{(1-\alpha_{M1})(1-\alpha_{F2})Q_2}{1-\alpha_M+\alpha_{M2}Q_2}-1\\&=(1-\alpha_{F1})\cdot\left(\frac{Q_1}{1-\alpha_{M2}Q_2}-1\right)+\frac{(1-\alpha_{M1})(1-\alpha_{F2})Q_2}{1-\alpha_{M1}Q_1}\\&=(1-\alpha_{F1})\cdot\frac{\alpha_{M2}Q_2-Q_2}{1-\alpha_{M2}Q_2}+\frac{(1-\alpha_{M1})(1-\alpha_{F2})Q_2}{1-\alpha_{M1}Q_1}\\&=Q_2\cdot\left(\frac{(1-\alpha_{M1})(1-\alpha_{F2})}{1-\alpha_{M1}Q_1}-\frac{(1-\alpha_{F1})(1-\alpha_{M2})}{1-\alpha_{M2}+\alpha_{M2}Q_1}\right).\end{aligned}$$

The expression enclosed in large parentheses is an increasing function of Q_1, so that only the following situations can arise: T_1 is globally (for all frequencies) superior or globally inferior to T_2 in mating success; T_1 is inferior if it is rare and superior if it is frequent (positive frequency dependence). For constant values of α, negative frequency dependence (i.e. whenever a type is rare, it is superior in mating success) thus cannot occur. At the marginal frequencies $Q_1=0$ and $Q_1=1$, the sign of the expression enclosed in large parentheses thus decides upon the possible ranking relationships between the mating successes of the two types. In the case where neither of the two types possesses a complete homotypic predisposition, the above results can be summarized as follows:

Superiority of type T_1	$\frac{1-\alpha_{F1}}{1-\alpha_{F2}}\leq 1-\alpha_{M1}$
Superiority of type T_2	$\frac{1-\alpha_{F1}}{1-\alpha_{F2}}\geq\frac{1}{1-\alpha_{M2}}$
Positive frequency dependence	$1-\alpha_{M1}<\frac{1-\alpha_{F1}}{1-\alpha_{F2}}<\frac{1}{1-\alpha_{M2}}$

Complete homotypic predisposition of a male or female type excludes the possibility of positive frequency dependence. If one type is completely homotypically predisposed in both sexes, or if both types are completely homotypically predisposed for the same sex, then both types have globally (over the whole range of frequencies) identical mating success.

In addition to the results listed in the above table, there are additional conditions for global superiority of a type or for positive frequency dependence. However, for global superiority of a type it is in any case necessary that its females have a stronger homotypic predisposition than the other type. The most important results of the above considerations can thus be summarized as in the following Table.

Result

Applying the conditions of the present model to two types, then the following situations arise for the effects of frequency independent homotypic predispositions on mating success:

- ▷ *Negative frequency dependence for the mating success of both types relative to one another is not possible; the only possibilities are global (over the range of all frequencies) superiority of one type or positive frequency dependence. In the latter case there exists exactly one frequency distribution for which both types have identical mating success.*
- ▷ *For global superiority of a type, it is characteristic that its female homotypic predisposition exceeds that of the other type; the superiority of such a type can be endangered if its male homotypic predisposition is too strong.*

Frequency dependent mating predisposition: As was mentioned earlier, the strength of mating predisposition of a type may, particularly in higher animals, be influenced by the frequencies of the types in the population. A simple example proceeds from the assumption that each individual originally has a mating predisposition which, however, is abandoned if the preferred type is not encountered after a certain number of mating contacts. The extent to which individuals of such a type mate according to their predisposition will thus depend on the number of mating contacts over which it maintains its predisposition and on the frequency of the preferred type in the population. More concretely, the following assumptions will be made in order to characterize this situation:

Model: All females are homotypically predisposed in their matings; male individuals show no mating predispositions and are polygynous. A female individual of type T_{Fi} mates with a male individual of its own type (T_{Mi}), if such a male turns up among the first n_i encounters during the cycle of simultaneous sexual maturity. If the preferred male type is not present among these n_i encounters, then the female mates with the next male it encounters. Hence, all females mate. The encounters are assumed to occur at random and independently of each other.

The probability that a T_{Mi}-male is present among the first n_i mating encounters of a T_{Fi}-female is equal to $1-(1-Q_i^M)^{n_i}$, so that T_{Fi}-females realize their mating predisposition with probability

$$\alpha_{Fi} = 1-(1-Q_i^M)^{n_i} \ .$$

This probability has to be inserted into the above general model of homotypic mating predisposition, where now, however, α_{Fi} is no longer constant and the α_{Mi}'s are identically equal to 0. As desired, α_{Fi} is now an increasing function of the frequency Q_i^M of T_{Mi}-males, and it is also an increasing function of the number of mating encounters over which T_{Fi}-females maintain their mating predisposition. According to equation (7.9a), the mating success of the male types is given by

$$h_{Mi} = \frac{1}{2Q_M} \cdot \left(\alpha_{Fi} \cdot \frac{Q_i^F}{Q_i^M} + 1 - \alpha_F \right) .$$

In contrast with constant (frequency independent) mating predispositions, even extreme deviations of 1:1 sex ratios of the types now cannot lead to unbounded and thus biologically unrealistic mating successes of the male types. It can be easily proven with the help of the rule of de l'Hospital that the quotient α_{Fi}/Q_i^M converges to n_i as Q_i^M approaches zero. However, in order to be able to study effects of the frequency dependence of the α_{Fi}'s on mating success in more detail (including particularly the situation for extreme frequencies), it is again advisable to consider the restriction to two types and a 1:1 sex ratio for each of the types.

For this case, one obtains for the difference in mating success between the two male types $(h_{M1} - h_{M2})2Q_M = \alpha_{F1} - \alpha_{F2} = (1-Q_2)^{n_2} - (1-Q_1)^{n_1}$. Hence, for fixed value of Q_M, the difference $h_{M1} - h_{M2}$ is an increasing function of Q_1, and, provided $n_1, n_2 > 0$, it reaches a value of –1 for $Q_1 = 0$ and a value of +1 for $Q_1 = 1$. Hence, there exists only the possibility of positive frequency dependence of the mating success of the two types relative to one another (the frequent type is superior in mating success to the rare type). Only if, for example, $n_1 = 0$ and $n_2 > 0$, the type T_1, which then mates at random, is globally inferior in mating success to the other type.

Result

If the male sex shows no mating predispositions and if individuals of the female sex maintain their homotypic mating predispositions only over a limited number of mating encounters, then the mating success of two types, relative to one another, is positively frequency dependent, i.e. the frequent type is always superior to the rare type.

Frequency dependent mating predisposition; a saturation model: The principles underlying the preceding model will now be extended by a phase of mating contacts that take place prior to the phase considered in this last model. Envision a situation where the first contacts between individuals of opposite sexes merely serve the purpose of allowing the females to gather information about the composition of their potential male mating partners. After this phase, and depending on the experience gathered, the originally present homotypic mating predisposition will be realized according to the system described in the preceding model. The experiencing phase will be characterized as follows:

Model: The polygynous males show no mating predispositions. A T_{Fi}-female does not mate during the first m_i contacts with males. If, among these contacts, only males of the same type (T_{Mi}-males) were encountered, then the female mates with the next male it encounters (**saturation**). Otherwise such a female mates with the first T_{Mi}-male it encounters during the next n_i contacts. If the preferred T_{Mi}-male does not show up during these contacts, the female (after $m_i + n_i$ contacts) mates with the next male it encounters. The encounters are assumed to occur at random and independently of each other.

Hence, during the experiencing phase, the homotypic mating predisposition of a female can become saturated, in which case the female mates at random. During the second phase, if initiated, the system of mating is identical to that considered the preceding model.

The probability of a T_{Fi}-female to experience saturation is $(Q_i^M)^{m_i}$. In case saturation did not take place (which has probability $1-(Q_i^M)^{m_i}$), T_{Fi}-females realize their homotypic mating predisposition with probability $1-(1-Q_i^M)^{n_i}$. Combining these probabilities, one obtains the probability with which T_{Fi}-females realize their homotypic mating preferences:

$$\alpha_{Fi} = [1-(Q_i^M)^{m_i}] \cdot [1-(1-Q_i^M)^{n_i}] \ .$$

All other homotypic matings, i.e. involving females that are either saturated or have abandoned their predisposition, occur at random. The general formulation of the model for homotypic mating predisposition is thus again applicable. With a 1:1 sex ratio for all types, equation (7.9b) states (under the present condition $\alpha_{Mi} \equiv 0$) that T_{Mi}-males are superior in mating success to T_{Mj}-males if and only if $\alpha_{Fi} > \alpha_{Fj}$ and thus $\alpha_{Fi}/\alpha_{Fj} > 1$. Hence, if the population consists of only two types, the last quotient can be written in the form

$$\frac{\alpha_{F1}}{\alpha_{F2}} = \frac{(1-Q_1^{m_1})(1-(1-Q_1)^{n_1})}{(1-Q_1^{n_2})(1-(1-Q_1)^{m_2})} \ .$$

Clearly, both types can be globally identical in mating success only if $m_1 = n_2$ and $n_1 = m_2$, i.e. if for each type the duration of its “saturation phase” is equal to the duration of the “mating phase” of the other type. Hence, identity in mating success of both types is not guaranteed by identity of their parameters m and n (i.e. $m_1 = m_2$ and $n_1 = n_2$) alone. On the other hand, if $m_1 > n_2$ and $m_2 < n_1$, global superiority of type T_1 results. Moreover, application of the rule of de l'Hospital to α_{F1}/α_{F2} at extreme frequencies yields the limits:

$$\begin{aligned} \frac{\alpha_{F1}}{\alpha_{F2}} &\longrightarrow \frac{n_1}{m_2} \quad \text{for } Q_1 \to 0 \\ \frac{\alpha_{F1}}{\alpha_{F2}} &\longrightarrow \frac{m_1}{n_2} \quad \text{for } Q_1 \to 1 \ . \end{aligned}$$

The following table summarizes the results that can be derived from the above considerations for the relationships between the mating success of two types (the m-values are supposed to be positive):

Global superiority of T_1	$m_1 \geq n_2$ and $m_2 < n_1$ or $m_1 > n_2$ and $m_2 \leq n_1$
Global superiority of T_2	$m_2 \geq n_1$ and $m_1 < n_2$ or $m_2 > n_1$ and $m_1 \leq n_2$
Superiority of the rare type	$n_1 > m_2$ and $n_2 > m_1$
Superiority of the frequent type	$n_1 < m_2$ and $n_2 < m_1$

As compared with the preceding model without saturation, it is conspicuous that the introduction of saturation allows for all ranking relationships in mating success between the two types. Since the major difference between the two models lies in the fact that saturation increases the possibilities for random mating, this effect may be suspected to be responsible for the occurrence of global superiority and negative frequency dependence in mating success of the two types relative to one another. However, neither the relationships between the duration of the mating phase (n_1 and n_2) nor for the duration of the saturation phase (m_1 and m_2) for the two types are involved in the creation of this result. Only the ratio $n : m$ of the duration of the mating phase of one type relative to that of the saturation phase of the other type is decisive.

For very long duration m_1 and m_2 of the saturation phase, the saturation model becomes identical to the preceding model without saturation, since in this case saturation cannot be reached. In this sense, the preceding model is a special case of the present saturation model. The major consequences of this model for differential mating success can be summarized as follows:

Result

For the present model of saturation of homotypic mating predisposition in the female sex and absence of mating predispositions in the male sex, the following results are characteristic for two types: At least at low frequencies, a type is superior in mating success if its females spend more time on the realization of their mating predisposition than the females of the other type spend on gathering information on the composition of their potential male mating partners. Only if their competitors do not apply the same strategy can they maintain their initial advantage globally.

NEGATIVE ASSORTATIVE MATING (HETEROTYPIC PREDISPOSITION)

Maintaining the present concept of mating predisposition, the results of the preceding section on positive assortative mating suggest that, for synchrony of sexual maturity, negative assortative mating can be expected as a consequence of some sort of heterotypic mating predisposition. As the counterpart of homotypic predisposition, **heterotypic mating predisposition** will be defined as the predisposition of an individual to mate with individuals that differ from its own type. All that counts in this concern is the state of being different in type, so that no distinction is made among these different types, i.e. no further mating predispositions exist. Moreover, not all individuals of a given type are required to possess the predisposition, and the Greek letter α will again be used to denote the extent to which the mating predisposition is realized among the individuals of a given type.

Notations

α_{Fi} := relative frequency of heterotypically predisposed individuals among all T_{Fi}-individuals;

α_{Mi} := relative frequency of heterotypically predisposed individuals among all T_{Mi}-individuals;

As opposed to homotypic mating predisposition, the potential mating partners of heterotypically predisposed individuals may comprise several types, provided there are more than two types in the population. Hence, two kinds of mating references have to be taken into consideration, one for non-predisposed individuals (R^c) and one for heterotypically predisposed individuals (R^h). The potential mating partners of all non-predisposed T_{Fi}-females consist of all males with the exception of the heterotypically predisposed T_{Mi}-males; this is a fraction $1 - \alpha_{Mi} Q_i^M$ of the total male population. Thus, the mating references of the non-predisposed female individuals of a given type result as

$$R^c_{Mj \triangleleft Fi} = \frac{Q_j^M (1 - \delta_{ij} \alpha_{Mi})}{1 - \alpha_{Mi} Q_i^M} \ .$$

The mating references for the non-predisposed male individuals of a given type are obtained in an analogous manner:

$$R^c_{Fj \triangleleft Mi} = \frac{Q_j^F (1 - \delta_{ij} \alpha_{Fi})}{1 - \alpha_{Fi} Q_i^F} \ .$$

On the other hand, the heterotypically predisposed T_{Fi}-females have to make their choice only among males differing from them in type (the proportion of which is $(1 - Q_i^M)$ among all males). By exchanging the roles of the sexes, one obtains the corresponding mating references for heterotypically predisposed T_{Mi}-males:

$$\begin{aligned} R^h_{Mj \triangleleft Fi} &= (1 - \delta_{ij}) \cdot \frac{Q_j^M}{1 - Q_i^M} \ , \\ R^h_{Fj \triangleleft Mi} &= (1 - \delta_{ij}) \cdot \frac{Q_j^F}{1 - Q_i^F} \ . \end{aligned}$$

The reasoning given in the preceding section on positive assortative mating, concerning the restrictions and classification with respect to the constancy of the parameters α and the circumstances of mating, applies equally to the present situation of heterotypic predisposition. The following models are therefore chosen in accordance with the principles applied to those of positive assortative mating.

Independence of female mating success from mating predispositions: This assumption again implies equal mating success for all female types, so that $P(T_{Fi}) = \frac{1}{2}Q_i^F$ for all i. Moreover, the heterotypically predisposed female individuals are assumed to mate at random with their potential mating partners specified by the above mating references R^h, while the non-predisposed female individuals mate at random with respect to the mating reference R^c. From this the mating norms

$$P_{Mj \triangleleft Fi} = \alpha_{Fi} \cdot R^h_{Mj \triangleleft Fi} + (1-\alpha_{Fi}) \cdot R^c_{Mj \triangleleft Fi}$$

result, which, after substitution for the mating references R^h and R^c, yields the mating frequencies

$$\begin{aligned} P(T_{Fi} \times T_{Mj}) =& Q_i^F \cdot Q_j^M \cdot \left[(1-\delta_{ij}) \cdot \frac{\alpha_{Fi}}{1-Q_i^M} \right. \\ & \left. + \frac{(1-\alpha_{Fi}) \cdot (1-\delta_{ij}\alpha_{Mi})}{1-\alpha_{Mi}Q_i^M} \right] \end{aligned} \tag{7.10a}$$

$$\begin{aligned} P(T_{Mj}) =& \frac{1}{2}Q_j^M \cdot \left[\sum_i \frac{\alpha_{Fi}Q_i^F}{1-Q_i^M} + \sum_i \frac{(1-\alpha_{Fi})Q_i^F}{1-\alpha_{Mi}Q_i^M} - \right. \\ & \left. - \frac{\alpha_{Fj}Q_j^F}{1-Q_j^M} - \frac{\alpha_{Mj}(1-\alpha_{Fj})Q_j^F}{1-\alpha_{Mj}Q_j^M} \right] . \end{aligned} \tag{7.10b}$$

Analogous application of the techniques used in the last section to the present situation again allows the question to be answered as to whether heterotypic mating predisposition implies negative assortative mating:

$$\begin{aligned} U_{Mj \triangleleft Fi} - U_{Mi \triangleleft Fi} &= \frac{\alpha_{Fi}}{1-Q_i^M} + \frac{1-\alpha_{Fi}}{1-\alpha_{Mi}Q_i^M} - \frac{(1-\alpha_{Fi})(1-\alpha_{Mi})}{1-\alpha_{Mi}Q_i^M} \\ &= \frac{\alpha_{Fi}}{1-Q_i^M} + \frac{(1-\alpha_{Fi})\alpha_{Mi}}{1-\alpha_{Mi}Q_i^M} \geq 0 \ . \end{aligned}$$

Thus, the heterotypic mating preferences of a female type always exceed its homotypic mating preferences. Only in the case where $\alpha_{Mi} = \alpha_{Fi} = 0$ are all heterotypic preferences identical to the homotypic preference, so that $U_{Mj \triangleleft Fi} = 1$ for all j, which means that T_{Fi}-females mate at random with all male types.

Considering the mating preferences of the male types one obtains for the difference in mating preference between homotypic and heterotypic matings

$$
\begin{aligned}
(U_{Fj\triangleleft Mi} - U_{Fi\triangleleft Mi}) \cdot \frac{2P(T_{Mi})}{Q_i^M} = & \\
&= \frac{\alpha_{Fj}}{1 - Q_j^M} + \frac{1 - \alpha_{Fj}}{1 - \alpha_{Mj} Q_j^M} - \frac{(1 - \alpha_{Fi})(1 - \alpha_{Mi})}{1 - \alpha_{Mi} Q_i^M} \\
&\geq \alpha_{Fj} + (1 - \alpha_{Fj}) - \frac{(1 - \alpha_{Fi})(1 - \alpha_{Mi})}{1 - \alpha_{Mi}} \\
&= \alpha_{Fi} \geq 0 \ .
\end{aligned}
$$

For the first estimation, the trivial inequalities $Q_i^M \leq 1$ and $Q_j^M \geq 0$ were used. Again all heterotypic mating preferences of a male type exceed its homotypic mating preference. Identity of all heterotypic mating preferences with the homotypic mating preference can occur only if the male sex is fixed for a single type (T_{Mi} in the present case) and if females of the same type have no mating predispositions ($\alpha_{Fi} = 0$). Hence, only in this probably biologically exceptional case can random mating of a male type with all female types be realized even though α_{Mi} need not be equal to 0. Otherwise, if at least two male types exist in the population, then $U_{Fj\triangleleft Mi} = U_{Fi\triangleleft Mi}$ can hold only for $\alpha_{Mi} = \alpha_{Mj} = \alpha_{Fj} = 0$. This need not imply random mating of T_{Mi}-males with all female types in the population, provided more than two male types exist. Moreover, since in this case $U_{Fi\triangleleft Mi} < 1$ and thus $U_{Fj\triangleleft Mi} < 1$, one recognizes that heterotypic mating preferences can be less than 1.

Result

If the female mating success does not depend on the mating predisposition and thus all female types have identical mating success, then heterotypic mating predisposition implies negative assortative mating in the sense that all heterotypic mating preferences of a type exceed its homotypic preference.

A female type can mate at random with all male types only if neither it nor its corresponding male type shows a mating predisposition. On the other hand, random mating with all female types is impossible for any male type if at least one male or female type is heterotypically predisposed. Only in the biologically exceptional case where the male sex is fixed for a single type can this type mate at random with all female types, provided its corresponding female type shows no mating predispositions.

As was previously done, the effects of heterotypic mating predisposition on mating success will be studied in more detail for the special case of two types, where, as far as dioecious populations are concerned, a 1:1 sex ratio is assumed for both types.

Two types with 1:1 sex ratio and equal female mating success: Considering that now $Q_2 = 1-Q_1$, one obtains for the difference in mating success between the two male types according to equation (7.10):

$$\begin{aligned} 2Q_M(h_{M1} - h_{M2}) &= \frac{\alpha_{M2}(1-\alpha_{F2})(1-Q_1)}{1-\alpha_{M2}(1-Q_1)} - \frac{\alpha_{M1}(1-\alpha_{F1})Q_1}{1-\alpha_{M1}Q_1} \\ &\quad + \frac{\alpha_{F2}(1-Q_1)}{Q_1} - \frac{\alpha_{F1}Q_1}{1-Q_1}\,. \end{aligned} \tag{7.11}$$

For given Q_M and constant values for α, this difference is a decreasing function of Q_1, and for $\alpha_{F1}, \alpha_{F2} > 0$ the difference ranges between $-\infty$ and $+\infty$. Hence, relative to one another, the mating success of the two types is negatively frequency dependent in the sense that the rare type is superior to the frequent type in mating success. However, the extreme values for the mating success indicate that again the assumption of constant mating predispositions is biologically realistic only to a limited extent. This aspect will be accounted for later by allowing the heterotypic mating predispositions to be frequency dependent. Global superiority (for all frequencies) of the type T_1, say, in mating success can be realized only if $\alpha_{F1} = \alpha_{M1} = 0$ and $\alpha_{F2} + \alpha_{M2} > 0$.

Result

For constant degrees of heterotypic mating predisposition and two types with identical mating success of the female types, the present model implies that the rare type is superior to the frequent type in male mating success, provided both types are heterotypically predisposed as females. In this case there exists exactly one frequency distribution at which both types have identical mating success. On the other hand, if one type is predisposed as female or as male but the other type shows no predisposition in either sex, then the nonpredisposed type is globally superior to the predisposed type.

Comparing the last statements with the corresponding results derived for homotypic mating predisposition, it turns out that these two forms of mating predisposition are not merely complementary with respect to their effects on mating success. While the absence of any mating predispositions is advantageous over heterotypic predispositions, the mere reversal is not true for homotypic predisposition. On the contrary, with homotypic mating predispositions there are various possibilities for global superiority of a type, provided this type exceeds the other in the extent of its female homotypic predisposition. Complementarity exists only with respect to the form of frequency dependence in mating success of the two types relative to one another, in that heterotypic mating predisposition does not allow for the existence of positive frequency dependence and negative frequency dependence is excluded for homotypic predisposition. Of course, even these statements need not remain true if any of the above stipulations (identical mating success in one sex and polygamy in the other sex, constant predispositions, etc.) is abandoned.

Frequency dependent mating predisposition; the saturation model: The specification of the model is completely analogous to that for homotypic mating predisposition and will, therefore, be repeated only briefly in connection with the special features of saturation for heterotypic mating predisposition:

Model: The polygynous male types show no mating predispositions; T_{Fi}-females do not mate during their first m_i encounters of males (saturation phase); if these females did not encounter males of their own type (T_{Mi}) during this phase they mate with the next male they encounter; otherwise, if they encountered a male of their own type during the saturation phase, they mate with the next male that shows up during the following n_i encounters and differs in type from their own; if such a male type does not show up during these n_i encounters, the female mates with the next male it encounters. The encounters are assumed to occur at random and independently of each other.

The parameters m_i and n_i again characterize the length of the saturation phase and the length of the phase during which the heterotypic mating predisposition is maintained, respectively. Very large (effectively infinite) values of m_i for all female types eliminate the effects of saturation on the mating system, so that the resulting model is equivalent to one without saturation where, for example, females try to realize their mating predispositions irrespective of their experiences prior to the mating phase

(n).

The probability α_{Fi} that a T_{Fi}-female realizes its heterotypic mating predisposition not by random mating (i.e. neither as a consequence of saturation during the m-phase nor of not having encountered the desired type during the n-phase) is

$$\alpha_{Fi} = [1 - (1 - Q_i^M)^{m_i}] \cdot [1 - (Q_i^M)^{n_i}] \ .$$

The special case of two types with a 1:1 sex ratio for each type will again provide more detailed insight into the effects of the present system of mating on mating success. For this case, equation (7.11) yields for the difference in mating success between the two male types (after substitution for α_{Fi} and setting $\alpha_{Mi} \equiv 0$):

$$\begin{aligned} 2Q_M \cdot (h_{M1} - h_{M2}) &= \frac{\alpha_{F2}(1-Q_1)}{Q_1} - \frac{\alpha_{F1} Q_1}{1-Q_1} \\ &= (1-Q_1)(1-Q_1^{m_2}) \cdot \frac{1-(1-Q_1)^{n_2}}{Q_1} - \\ &- Q_1[1-(1-Q_1)^{m_1}] \cdot \frac{1-Q_1^{n_1}}{1-Q_1} \ . \end{aligned}$$

In this equation $[1 - (1 - Q_1)^{n_2}]/Q_1$ is a decreasing function of Q_1, provided $n_2 > 1$, and $(1 - Q_1^{n_1})/(1 - Q_1)$ is an increasing function of Q_1, provided $n_1 > 1$. Hence, for given Q_M, the difference between the male mating successes is a decreasing function of Q_1. Applying the rule of de l'Hospital it turns out that the difference $h_{M1} - h_{M2}$ varies between the extreme values $n_2/(2Q_M)$ (for $Q_1 = 0$) and $-n_1/(2Q_M)$ (for $Q_1 = 1$). Since the parameters m_1 and m_2 characterizing the saturation phase do not appear in these extreme values, one concludes that the observation of negative frequency dependence in mating success of the two types relative to each other is not affected by the presence or absence of saturation in the present model. Moreover, this result is identical to that obtained for constant values α of heterotypic mating predisposition.

Result

For two types, the particular form of frequency dependence of female heterotypic mating predisposition assumed in the present model implies no qualitatively new results as compared to the situation of constant heterotypic mating predispositions: The rare type is superior in mating success to the frequent type irrespective of whether saturation does or does not take place; there exists exactly one frequency distribution for which the two types have identical mating success.

8. Selection with two alleles and two types

All of the models treated in chapter 7 were analysed in more detail for the special case of two types, with particular reference to their ranking in mating success. The present objective is to inquire into the significance of these results on reproductive success for evolutionary success (recall the remarks at the beginning of chapter 4). This requires specification of modes of inheritance, the gene action systems of which produce exactly two different phenotypes. An infinite number of such modes is conceivable, including, for example, purely cytoplasmic (extranuclear), unisexual inheritance (mostly via the female gametes), nuclear inheritance involving an arbitrary number of gene loci (which requires epistasis to limit the number of phenotypes to two), or nuclear-cytoplasmic inheritance.

From this wealth of possibilities, the simplest mode of inheritance, excluding haploid inheritance, will be considered, namely a single nuclear, diploid, autosomal gene locus at which only two alleles (denoted by A_1 and A_2) exist. There are two modes of gene action which produce two phenotypes: complete dominance of A_1, say, over A_2, so that the genotypes A_1A_1 and A_1A_2 are phenotypically equivalent; and phenotypic equivalence of the two homozygote genotypes A_1A_1 and A_2A_2, which leaves the heterozygote genotype A_1A_2 to code for the second phenotype. Hence, genetically, three types exist in each case, but two of these are completely indistinguishable with respect to their effects on the mating process and are thus mating equivalent (see section 1.5).

Since the influence of mating equivalence of two types on their respective mating success has not as yet been considered, this will be briefly made up for. Subsequently, the question will be answered as to whether, under the above two modes of inheritance, reproductive success converts into evolutionary success. For this purpose it will be stipulated that populations be of effectively infinite size and reproduce in separated generations, that genotypic frequencies be scored at the zygotic stage in each generation, that regular segregation obtain within the zygote production of each mating type, and that mating events be defined by the fusion of gametes. Hence, the transition equations (6.1) will again be obligatory.

Mating equivalence and mating success: Excluding, for the present, individual self-mating, condition (c) for mating equivalence of two types

T_1 and T_2 (see section 1.5) yields

$$\frac{1}{2}(1+\delta_{i1})P(T_1\times T_i)\cdot R_{2\triangleleft i}=\frac{1}{2}(1+\delta_{i2})P(T_2\times T_i)\cdot R_{1\triangleleft i}\quad\text{for all } i.$$

When applied to dioecious populations with natural mating references, this equation takes the form

$$P(T_{F1}\times T_{Mi})\cdot Q_2^F = P(T_{F2}\times T_{Mi})\cdot Q_1^F\quad\text{for all } i$$

for mating equivalence of the female types T_{F1} and T_{F2}, and

$$P(T_{M1}\times T_{Fi})\cdot Q_2^M = P(T_{M2}\times T_{Fi})\cdot Q_1^M\quad\text{for all } i$$

for mating equivalence of the male types T_{M1} and T_{M2}.

Summation over i yields for the female types $P(T_{F1})Q_2^F = P(T_{F2})Q_1^F$ and for the male types $P(T_{M1})Q_2^M = P(T_{M2})Q_2^M$, so that $h_{F1}=h_{F2}$ and $h_{M1}=h_{M2}$. The corresponding result for cosexual populations is obtained by setting $Q_i^M = Q_i^F = Q_i$, which implies $h_i = [P(T_{Fi})+P(T_{Mi})]/Q_i$. It turns out that again $h_1 = h_2$. Hence, as was to be expected under the stipulation of natural mating references, *mating equivalence of two types implies equality of their mating success.* The same result is obtained when allowing for individual self-mating, in which case the natural cross-mating references are given by $R^c_{i\triangleleft j} = (1-P_i^s)Q_i/(1-P^s)$ (see sections 1.5 and 5.2 following equation (5.6)). The computations are more tedious but straightforward.

8.1 Complete dominance of an allele

In order to retain the previously introduced notation, the genotype A_iA_j will be denoted by T_{ij}, and whenever the sexual specificity of the carrier of this genotype is explicitly considered, the notations T_{Fij} and T_{Mij} are applied to distinguish between the female and male sex, respectively. Analogously, the mating success of a genotype is denoted as h_{ij}, h_{Fij} or h_{Mij}. According to equation (6.1), among the zygotes resulting from the mating events, the relative frequency q_i' of the allele A_i ($i=1,2$) is

$$q_i' = P(T_{ii})+\frac{1}{2}P(T_{12}) = h_{ii}\cdot Q_{ii}+\frac{1}{2}h_{12}\cdot Q_{12}\ . \qquad (8.1a)$$

Taking into account that $P(T_{ij}) = P(T_{Fij}) + P(T_{Mij})$, the inclusion of sexual specificity into equation (8.1a) yields

$$\begin{aligned} q_i' =& P(T_{Fii}) + P(T_{Mii}) + \frac{1}{2}\left[P(T_{F12}) + P(T_{M12})\right] \\ =& \left(h_{Fii} \cdot Q_{ii}^F + \frac{1}{2} h_{F12} \cdot Q_{12}^F\right) \cdot Q_F \\ &+ \left(h_{Mii} \cdot Q_{ii}^M + \frac{1}{2} h_{M12} \cdot Q_{12}^M\right) \cdot Q_M \ . \end{aligned} \tag{8.1b}$$

Since the gene locus considered is assumed to be autosomal, the requirement that A_1 be completely dominant over A_2 applies to all sexual types. Hence, if sex specificity enters the typification of the gametes or the members of a dioecious population, the two female types T_{F11} and T_{F12} as well as the two male types T_{M11} and T_{M12} are mating equivalent. Thus, according to the preceding result on mating equivalence, $h_{F11} = h_{F12}$ and $h_{M11} = h_{M12}$, which implies $h_{11} = h_{12}$ for cosexual populations as well as for any situation where sex specificity is not explicitly accounted for. The last statement follows directly from the generally valid relationship $h_i = (h_{Fi}Q_{Fi} + h_{Mi}Q_{Mi})/Q_i$, where $Q_i = Q_{Fi} + Q_{Mi}$ and, additionally, for cosexual populations $Q_{Fi} = Q_{Mi}$. Complete dominance of A_1 thus leads (according to equations (8.1a)) to the basic transition equation

$$q_1' = h_{11} \cdot q_1 \ , \tag{8.2a}$$

and, in the case where the sex specificity of gametes or members of a dioecious population is explicitly accounted for, equation (8.1b) yields

$$q_1' = h_{F11} \cdot q_1^F \cdot Q_F + h_{M11} \cdot q_1^M \cdot Q_M \ . \tag{8.2b}$$

Here, the sex specific allele frequencies $q_1^F = Q_{11}^F + \frac{1}{2}Q_{12}^F$ and $q_1^M = Q_{11}^M + \frac{1}{2}Q_{12}^M$ refer to the allele frequencies among all female and male members, respectively, in the population before mating takes place. Because of the assumption of natural mating references, these frequencies correspond to those in the male and female mating reference, respectively.

Under the additional assumption of a 1:1 sex ratio for both types prior to mating (which is equivalent to the assumption that in both sex specific mating references the frequency distributions of the types are the same), one obtains for the allele frequencies $q_i^F = q_i^M = q_i$, so that equation (8.2b) simplifies to

$$q_1' = (h_{F11} \cdot Q_F + h_{M11} \cdot Q_M) \cdot q_1 \ . \tag{8.2c}$$

Moreover, if in one sex, the female sex say, both types have equal mating success (as was assumed in the models on mating predisposition in section 7.2), $h_{F11} = 1/(2Q_F)$ holds, so that in this case

$$q_1' = \left(\frac{1}{2} + h_{M11} \cdot Q_M\right) \cdot q_1 \ . \qquad (8.2d)$$

Although the transition equations (8.2) reflect only the changes in allele (not genotypic) frequencies, they suffice to state some important relationships between reproductive and evolutionary success which are characteristic for the presently assumed mode of inheritance in general, and which apply in particular to the models of assortative mating formulated for two types in chapter 7. The two types considered in these models correspond to the present types T_{11} and T_{22}, T_{F11} and T_{F22}, or T_{M11} and T_{M22}. Equation (8.2a) applies to cosexual populations and is thus particularly suited for the models on asynchrony in sexual maturity treated in section 7.1. Equations (8.2c) and (8.2d) refer to the situation of dioecious populations with a 1:1 sex ratio for all types (or of the corresponding cosexual populations), which makes these equations directly applicable to the models on synchrony of sexual maturity treated in section 7.2. In particular, equation (8.2d) reflects the models built upon the assumption of independence of female mating success from mating predispositions.

Superiority and inferiority of type T_{11} ($= T_{12}$) to type T_{22} in mating success is equivalent to $h_{11} > 1$ and $h_{11} < 1$, respectively. According to equation (8.2a), superiority and inferiority of the dominant type (A_1A_1, A_1A_2) to the recessive type (A_2A_2) is thus directly associated with an increase and decrease, respectively, in frequency of the dominant allele. This result also applies to the case of a dioecious population with 1:1 sex ratios for all types and identity of mating success for all female types; in this case type T_{11} is superior in mating success if and only if $h_{M11}Q_M > \frac{1}{2}$, which implies $q_1' > q_1$ according to equation (8.2d).

Consequently, all of the models for two types treated in section 5.3 and in chapter 7 are covered by the transition equations (8.2), and these equations furthermore give rise to the general statement formulated in the following Table.

Result

If a population consists of two types, the mode of inheritance of which can be specified by two alleles at a diploid, autosomal gene locus with complete dominance of one of the two alleles and regular segregation among the zygotes, then superiority of one type over the other in mating success is equivalent to an increase in relative frequency of that allele which characterizes the superior type.

Clearly, the increase in relative frequency of an allele is directly associated with superiority in mating success of the type which is homozygous for this allele. Hence, this rule does not depend on whether the allele is dominant (in which case A_1A_1 and A_1A_2 equally characterize the superior type) or recessive (in which case A_2A_2 is the superior type). Therefore, the conformity of evolutionary and reproductive success evident here (on the basis of allele frequencies) does not, at least not qualitatively, depend on whether the dominant or the recessive type is superior. However, with respect to quantitative aspects of the evolutionary dynamics, dominance and recessivity of the superior type may have substantially different consequences. Of primary concern here are the speed of increase of an allele in frequency and the number of generations until fixation of the superior type. In addition to the special characteristics of the mating system, these dynamical aspects depend on the initial frequencies of the three genotypes (not just of the two types).

The models for two types treated in section 5.3 and chapter 7 were all characterized with respect to the mode of frequency dependence of the mating success of the two types relative to each other. For fixed model parameters, these models all allowed for a classification into global superiority of one type in mating success over the other (for all frequencies), negative frequency dependence (the rare type is superior in mating success to the frequent type), and positive frequency dependence (the rare type is inferior in mating success to the frequent type). For the presently considered mode of inheritance, these modes of frequency dependence imply as evolutionary consequences global fixation of the superior type, protected polymorphism (both types persist in the population), and facultative fixation of either type, respectively. The latter (**facultative fixation**) means that whenever and for whatever reasons one of the types becomes rare, irrespective of which of the two types is concerned, this type will eventually disappear from the population. The opposite is the **protected polymor-**

phism, in which case a type increases in frequency in the course of the generations after it has been reduced due to temporarily acting forces, and this applies equally to both types. In general, this need not imply that, when undisturbed, the types converge to a stable ratio of frequencies in the course of the generations. The frequencies of the types may just as well continually oscillate around an equilibrium state, without running into the danger of disappearing from the population. Since in an equilibrium state the allele frequencies no longer change, both types must have identical mating success for equilibrium frequencies, as follows from the equations (8.2). Moreover, recall that in all of the above-cited models negative or positive frequency dependence entailed the existence of exactly one set of frequencies at which both types showed equal mating success. However, problems of convergence to equilibria will not be treated here, since each special model would require a separate analysis, which would make it difficult to arrive at any generally valid conclusions on the stability of equilibria. It cannot be ruled out yet that such conclusions can be arrived at with the help of a detailed characterization of the mating frequencies or the mating preferences.

Of greater interest is the question as to whether changes in the mode of inheritance of the two types can invalidate the above correspondence between reproductive and evolutionary success. Continuing the preceding style of reasoning, this will be shown in the next section to actually be the case for a very simple change, namely re-assignment of the three genotypes at a biallelic gene locus to the two types.

8.2 Mating equivalence of the homozygotes

Complete dominance means mating equivalence among all carriers of the dominant allele. Given two (pheno-) types, the only alternative mode of inheritance based on a biallelic diploid gene locus consists in replacing the mating equivalence of one homozygote and the heterozygote by mating equivalence of the two homozygotes. This alternative mode of inheritance will now be considered. However, while complete dominance is a very well known mode of gene action, equivalence of the homozygotes, where both genotypes have no allele in common, needs some explanation and justification when viewed as a system or mode of gene action.

A very simple explanation can be obtained by taking ontogenetic and/or ecological factors into consideration. Envision, for example, a situation where all individuals are subject to the action of an environmental factor which successively varies in time between two levels and which can thus affect the ontogenesis of each individual. Furthermore, suppose that one of the alleles reacts more strongly to the first than to the second level of the environmental factor, while the other allele reacts in exactly the reverse order. Hence, when viewed over the whole span of time, in both homozygotes the sum of the gene activities is the same, so that they could express the same overall phenotype. The combination of the two alleles in a heterozygous individual could then, due to non-linear interactions of the alleles, produce a phenotype which differs from that coded for by the two homozygous genotypes.

Non-linear forms of interaction of two alleles may arise with dimeric enzymes, for example, since here the heterozygote produces an alloenzyme (hybrid enzyme) in addition to the enzymes of the two corresponding homozygotes. Particularly in this case, it is easily conceivable that only the additional alloenzyme triggers a difference in effect. In both examples the resulting mode of inheritance would thus again be based on a single gene locus with two alleles, but it would substantially differ from that of complete dominance.

The transition equation (8.1a) for the allele frequencies applies generally to the case of two alleles at an autosomal gene locus with regular segregation and thus obtains for the present case in particular. Because of the mating equivalence of the two homozygotes A_1A_1 and A_2A_2, the mating successes of these two genotypes are identical, i.e. $h_{11} = h_{22} =: h_{Ho}$ (the subscript Ho is used to denote homozygosity without reference to the alleles involved). Forming the difference $q_1' - q_2'$ between the frequencies of the two alleles in the next generation and considering that $q_1 - q_2 = Q_{11} - Q_{22}$ yields the transition equation

$$q_1' - q_2' = h_{Ho} \cdot (q_1 - q_2) \ . \tag{8.3}$$

Superiority and inferiority in mating success of the homozygote (T_{Ho}) as compared to the heterozygote (T_{12}) type is equivalent to $h_{Ho} > 1$ and $h_{Ho} < 1$, respectively. Since the heterozygote type can never become fixed in the population, the homozygote type is always present even if it is globally inferior in mating success, which is in clear contradiction to the situation of complete dominance. Hence, the only evolutionary events that can occur with equivalence of the homozygotes are protected polymorphism or fixation of the homozygote type (including the possibility that only one or both homozygous genotypes are present). The following cases can be distinguished:

- ▷ *Global superiority of the homozygous type T_{Ho}:* Since $h_{Ho} > 1$ in this case, the difference $|q_1 - q_2|$ increases continually over the generations according to equation (8.3), provided $q_1 \neq q_2$ initially. Hence, fixation of that allele takes place, which was originally the more frequent. From a genetic point of view, this is a situation of facultative fixation, while from the viewpoint of the phenotypes, fixation of the type with the greater mating success takes place. So far, reproductive and evolutionary success concur on the level of the phenotype.

- ▷ *Global superiority of the heterozygous type T_{12}:* In this case, the concurrence of evolutionary and reproductive success is of limited validity. $h_{12} > 1$ is equivalent to $h_{Ho} < 1$, so that, according to equation (8.3), the difference $q_1 - q_2$ converges to 0 in the course of the generations, i.e. both allele frequencies converge to $\frac{1}{2}$. At this state the heterozygote cannot disappear from the population, since it is either formed by matings between the homozygous genotypes or, because of its positive mating success, by its matings with either homozygote or with itself. Furthermore, the mating equivalence of the two homozygous genotypes implies that a situation in which matings between the two homozygotes are inhibited entails inhibition of matings between individuals of the same homozygous genotype. Hence, in such a situation all homozygotes are formed by matings between heterozygous individuals, so that a stable genotypic equilibrium results in which the heterozygote has frequency $\frac{1}{2}$, and both homozygotes have frequency $\frac{1}{4}$. Consequently, both the genotypic and the phenotypic polymorphism are protected.

- ▷ *Negative frequency dependence:* Now $h_{Ho} < 1$ for small values of Q_{12} and $h_{Ho} > 1$ for large values. It follows immediately from the above considerations of global superiority of the homozygous type that large values for Q_{12} can be maintained only for a limited number of generations. Consequently, in the course of the generations, h_{Ho} must decrease to a value less than or equal to 1. Thus, the heterozygous type can disappear from the population only if either initially $q_1 = q_2 = \frac{1}{2}$ or if the dynamics are such that h_{Ho} remains properly below 1, in which case the allele frequencies would converge to $\frac{1}{2}$. Hence, the decision on the maintenance of the heterozygote is made in the invariant frequency region $q_1 = q_2 = \frac{1}{2}$. However, in this region the above results for global superiority of the heterozygote apply, so that again both the phenotypic and the genotypic polymorphism are protected.

▷ *Positive frequency dependence:* In this case $h_{Ho} < 1$ for large values of Q_{12} and $h_{Ho} > 1$ for small values. Starting with a low frequency of the heterozygous type and $q_1 \neq q_2$, the difference $|q_1 - q_2|$ increases in the next generation, and this process would continue in all of the following generations, provided Q_{12} was sufficiently small at the outset. Under this assumption facultative fixation would result, and the heterozygous type would ultimately disappear from the population. On the other hand, if Q_{12} was sufficiently large at the outset, cases are conceivable in which $h_{Ho} \leq 1$ continues to hold in the following generations, so that the heterozygous type would persist in the population. Hence, for positive frequency dependence, additional characteristics of the respective model decide on the persistence of the heterozygous type.

Result

For the case of mating equivalence of both homozygous genotypes, the homozygous (pheno-) type persists in the population irrespective of its mating success. Under this mode of inheritance the principle of the concurrence of reproductive and evolutionary success does not apply in all cases.

The heterozygous type cannot disappear from the population if it is globally superior in mating success or if negative frequency dependence in mating success of the two types relative to one another is realized.

Global superiority of the homozygous type implies extinction for the heterozygous type. Only in this case does the principle of the concurrence of reproductive and evolutionary success hold without restrictions.

For positive frequency dependence in mating success of the two types relative to one another, the heterozygous type disappears from the population if it already started at low frequency. For large initial frequency, however, it cannot be ruled out that special systems of mating will prevent the loss of the heterozygous type.

The last statement concerning the possibility for more complicated dynamics of the genotypic and phenotypic frequencies in the presence of positive frequency dependence points at the necessity of extending the above analysis of changes in allele frequency to an analyis of genotypic frequencies.

Dynamics of genotypic and phenotypic frequencies: The models of chapter 7 will now form the basis for an analysis of the dynamics of the genotypic and phenotypic frequencies. It will therefore be assumed that *individual self-mating does not take place*, and, as far as dioecious populations are concerned, that among the zygotes all three genotypes show 1:1 sex ratios, i.e. $Q^F_{ij} = Q^M_{ij} = Q_{ij}$. Thus, the relative frequency of the homozygous (pheno-) type T_{Ho} is $Q_{Ho} = Q_{11} + Q_{22}$, and the natural mating references of the genotypes are $R^c_{ij \lhd kl} = R_{ij \lhd kl} = Q_{ij}$ $(i, j, k, l = 1, 2)$. By equations (1.6) the mating equivalence of the two homozygotes yields for the mating frequencies:

$$\begin{aligned}
P(T_{11} \times T_{22}) &= P(T_{Ho} \times T_{Ho}) \cdot \frac{2Q_{11}Q_{22}}{Q^2_{Ho}}\,, \\
P(T_{ii} \times T_{ii}) &= P(T_{Ho} \times T_{Ho}) \cdot \left(\frac{Q_{ii}}{Q_{Ho}}\right)^2\,, \\
P(T_{ii} \times T_{12}) &= P(T_{Ho} \times T_{12}) \cdot \frac{Q_{ii}}{Q_{Ho}}\,, \\
P(T_{ii}) = P(T_{Ho}) &\cdot \frac{Q_{ii}}{Q_{Ho}} \quad \text{for } i = 1 \text{ or } i = 2\,.
\end{aligned}$$

The first equation results from (1.6c), the second by application of the first to (1.6b), the third from (1.6a), and the fourth from (1.6d). For regular segregation among the offspring of each mating type one thus obtains the transition equations (8.4).

$$\begin{aligned}
Q'_{ii} =& P(T_{ii} \times T_{ii}) + \frac{1}{2}P(T_{ii} \times T_{12}) + \frac{1}{4}P(T_{12} \times T_{12}) \\
=& \frac{Q_{ii}}{Q_{Ho}} \cdot \left[P(T_{Ho} \times T_{Ho}) \cdot \frac{Q_{ii}}{Q_{Ho}} + \frac{1}{2}P(T_{Ho} \times T_{12})\right] \qquad (8.4a) \\
&+ \frac{1}{4}P(T_{12} \times T_{12})\,,
\end{aligned}$$

$$\begin{aligned}
Q'_{12} =& 1 - Q'_{11} - Q'_{22} = \frac{2Q_{11}Q_{22}}{Q^2_{Ho}} \cdot P(T_{Ho} \times T_{Ho}) \\
&+ \frac{1}{2}(1 - P(T_{Ho} \times T_{Ho})) \qquad (8.4b) \\
=& \frac{1}{2}\left[1 - \left(\frac{Q_{11} - Q_{22}}{Q_{Ho}}\right)^2 \cdot P(T_{Ho} \times T_{Ho})\right]\,,
\end{aligned}$$

$$\begin{aligned} q_i' &= P(T_{ii}) + \frac{1}{2}P(T_{12}) = \frac{Q_{ii}}{Q_{Ho}} \cdot P(T_{Ho}) + \frac{1}{2}P(T_{12}) \\ &= \left(\frac{Q_{ii}}{Q_{Ho}} - \frac{1}{2}\right) \cdot P(T_{Ho}) + \frac{1}{2}\ . \end{aligned} \tag{8.4c}$$

The most characteristic feature of these transition equations probably consists in the observation that, for $q_1 = q_2 = \frac{1}{2}$, immediately in the next generation the frequency of the heterozygote is $\frac{1}{2}$, while each of the homozygous genotypes has frequency $\frac{1}{4}$. It is worth mentioning that these frequencies constitute Hardy-Weinberg proportions, and they are attained irrespective of whether or not assortative mating takes place. The result follows directly from the transition equation for the heterozygote frequency Q_{12} (recall that $q_1 - q_2 = Q_{11} - Q_{22}$ holds by definition). According to the preceding derivations, this equilibrium state will be approached from all (polymorphic) initial frequencies during the course of the generations if, for example, the heterozygous type is globally superior in mating success to the homozygous type. However, it has to be emphasized that this equilibrium state exists only under the present assumption of absence of individual self-mating. The presence of individual self-mating is likely to change the picture (compare the results in chapter 6).

The attractivity of the **central equilibrium** $Q_{11} = Q_{22} = \frac{1}{4}$, $Q_{12} = \frac{1}{2}$ depends, above all, upon the mating success of the two types at this frequency distribution, where, because of the mating equivalence of the two homozygotes, distinction must be made only between the frequencies Q_{12} and Q_{Ho}, but not between Q_{11} and Q_{22}. This follows from the fact that, for the frequency condition $Q_{12} = Q_{Ho} = \frac{1}{2}$ and mating success $h_{Ho} < 1$ (or equivalently $h_{12} > 1$), the population approaches the central equilibrium by equation (8.3), provided it starts with frequencies Q_{12} (or Q_{Ho}) close to $\frac{1}{2}$. In this case the central equilibrium is at least locally attractive. On the other hand, if $h_{Ho} > 1$ for $Q_{12} = Q_{Ho} = \frac{1}{2}$, the population can never come arbitrarily close to the central equilibrium when it starts with initial frequencies $Q_{11} \neq Q_{22}$. This holds even for the case where, for sufficiently large deviation of the heterozygote frequency from $\frac{1}{2}$, the pertinent mating success of the homozygous type is less than 1 ($h_{Ho} < 1$).

These findings allow the previous results on the effects of negative and positive frequency dependence of the mating successes on the dynamics of the genotypic and phenotypic frequencies to be made more precise. In this respect, it is important to consider that the heterozygote cannot exceed a frequency of $\frac{1}{2}$ after the first generation (see equation (8.4)). For negative frequency dependence of the mating successes, the polymorphism is protected, and if in addition $h_{Ho} < 1$ for $Q_{Ho} = \frac{1}{2}$, then global convergence of the genotypic frequencies to the central equilibrium is guaranteed. In contrast, for positive frequency dependence, the permanent coexistence of both types in the population can be definitely ruled out if $h_{Ho} > 1$ holds for $Q_{Ho} = \frac{1}{2}$. From a genetic point of view, this case implies facultative fixation.

Result

If, initially, both alleles are equally frequent ($q_1 = q_2 = \frac{1}{2}$)*, then an equilibrium state is attained in the next generation; in this state the heterozygote has frequency* $\frac{1}{2}$*, and each of the two homozygotes has frequency* $\frac{1}{4}$ *each (central equilibrium). After the first generation the heterozygote cannot exceed a frequency of* $\frac{1}{2}$*.*

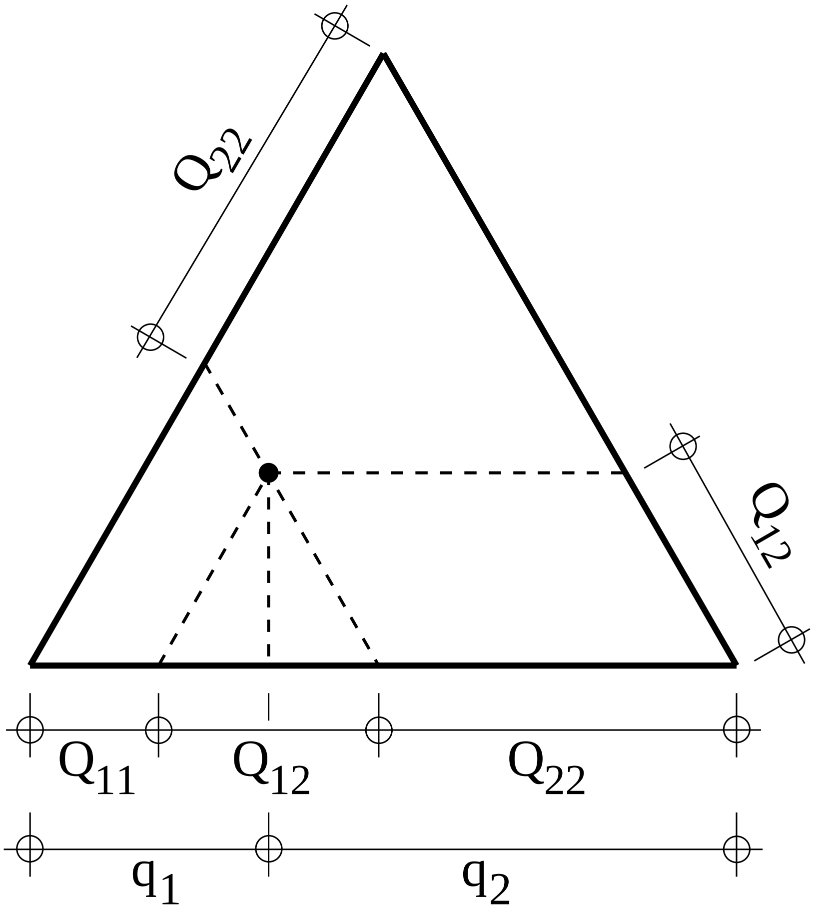
Negative frequency dependence in mating success of the two types relative to one another implies global convergence to the central equilibrium for all polymorphic initial conditions, provided the heterozygous type is superior in mating success to the homozygous type when both types are equally frequent ($Q_{12} = Q_{Ho} = \frac{1}{2}$)*. Such global convergence occurs without any restrictions for global superiority of the heterozygous over the homozygous type in mating success.*

Genetically facultative fixation – and thus loss of the heterozygous type – occurs for positive frequency dependence of the mating success of the two types relative to one another, if initially both alleles are not equally frequent, and if for equal frequency of the two types the homozygous is superior to the heterozygous in mating success.

As compared with the situation where individual self-mating is included, the exclusion of individual self-mating allows for a further reduction of the cases, in which the asymptotic dynamics of the genotypic frequencies cannot be generally analyzed, to positive frequency dependence with $h_{Ho} < 1$ for $Q_{12} = Q_{Ho} = \frac{1}{2}$ and to negative frequency dependence with $h_{Ho} > 1$ for $Q_{12} = Q_{Ho} = \frac{1}{2}$. These cases will now be briefly considered with the help of numerical examples based on the models of homotypic and heterotypic mating predisposition introduced in section 7.2.

An elegant graphical representation of the numerical results on the dynamics is provided by the so-called **de Finetti triangle** (de Finetti 1926), in which the three relative genotypic frequencies appear as a single point

Figure 2



The de Finetti triangle

in the area of an equilateral triangle with sides of length 1. The three coordinates of each point can be specified in different ways and correspond to the relative frequencies of the three genotypes (see Figure 2). This form of specification of the coordinates deviates somewhat from the usually applied form, but, it has the advantage of measuring directly (without any transformation) the size of the genotypic as well as the allelic frequencies. All of the following numerical examples will be illustrated with the help of this graphical representation.

Homotypic mating predisposition: Since the genotypic frequencies are completely determined by specification of the frequency Q_{12} of the heterozygote and the frequency q_1 of the allele A_1, according to the equations (8.4) the dynamics can be analyzed by merely computing $P(T_{Ho} \times T_{Ho})$ and $P(T_{Ho})$. From the equations (7.8) one thus obtains

$$\begin{aligned}
P(T_{Ho} \times T_{Ho}) =& \alpha_{FHo} \cdot Q_{Ho} + \frac{1-\alpha_{FHo}}{1-\alpha_{M12} \cdot Q_{12}} \cdot Q_{Ho}^2 \, , \\
P(T_{Ho}) =& \frac{1}{2}(1+\alpha_{FHo}) \cdot Q_{Ho} + \frac{1}{2}\frac{1-\alpha_{FHo}}{1-\alpha_{M12} \cdot Q_{12}} \cdot Q_{Ho}^2 + \\
&+ \frac{1}{2}\frac{(1-\alpha_{MHo})(1-\alpha_{F12})}{1-\alpha_{MHo} \cdot Q_{Ho}} \cdot Q_{Ho} \cdot Q_{12} \, .
\end{aligned}$$

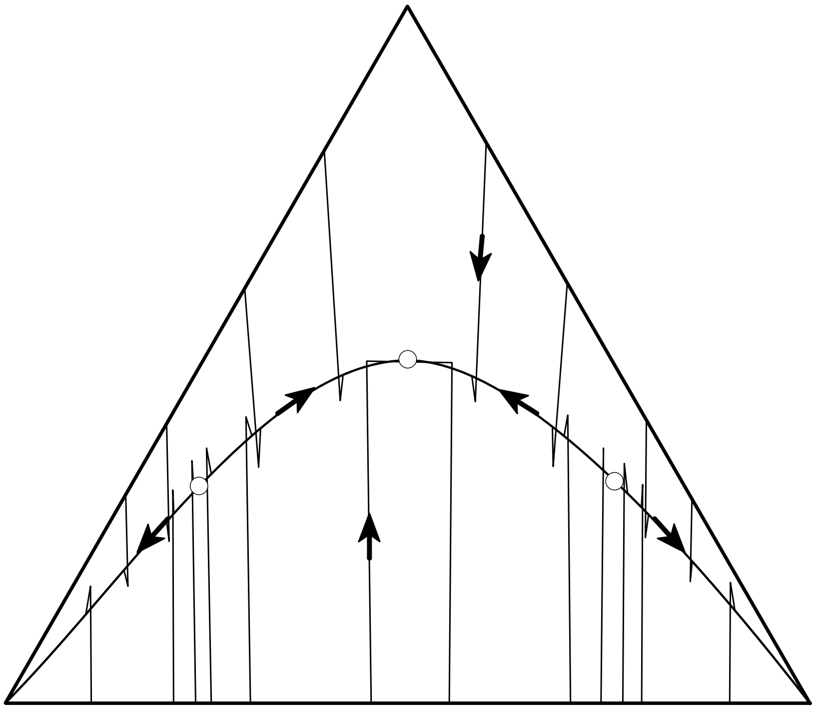
Recall that for constant homotypic mating predispositions only two situations are possible with respect to the ranking in mating success, namely global superiority of one type over the other or positive frequency dependence of each type relative to the other. The latter situation is realized if and only if $1-\alpha_{MHo} < (1-\alpha_{FHo})/(1-\alpha_{F12}) < (1-\alpha_{M12})^{-1}$ holds. As was shown above, for this situation only the case $h_{Ho} < 1$ for $Q_{12} = Q_{Ho}$ deserves particular interest since it cannot be treated satisfactorily with the help of the previous general analysis. Letting h_{Ho}^* denote the value that h_{Ho} assumes when $Q_{12} = Q_{Ho} = \frac{1}{2}$, one obtains

$$2 \cdot (h_{Ho}^* - 1) = \frac{1-\alpha_{MHo}}{2-\alpha_{MHo}} \cdot (1-\alpha_{F12}) - \frac{1-\alpha_{M12}}{2-\alpha_{M12}} \cdot (1-\alpha_{FHo}) \, .$$

It can be taken from this representation that positive frequency dependence is realized together with $h_{Ho}^* < 1$ if, for example, one of the following conditions holds: (1) $\alpha_{M12} < \alpha_{MHo}$, $\alpha_{FHo} < \alpha_{F12} < 1$ and $1-\alpha_{M12} < (1-\alpha_{F12})/(1-\alpha_{FHo})$; (2) $0 < \alpha_{M12} = \alpha_{MHo} < 1$, $\alpha_{FHo} < \alpha_{F12} < 1$ and $1-\alpha_{M12} < (1-\alpha_{F12})/(1-\alpha_{FHo})$; (3) $\alpha_{FHo} = \alpha_{F12} < 1$ and $0 < \alpha_{M12} < \alpha_{MHo} < 1$. Figure 3 demonstrates the dynamics of the genotypic frequencies in the de Finetti triangle for a set of parameters α satisfying one of these conditions (condition (1)); different initial conditions for the genotypic frequencies are used in order to give a more complete idea of the dynamics.

The most conspicuous observation is that two symmetrically located polymorphic equilibrium states appear to exist in addition to the locally stable central equilibrium. These putative equilibria divide the state space of genotypic frequencies in such a way that initial conditions located between these equilibria belong to the domain of attraction of the central equilibrium, while other initial conditions lead to asymptotic fixation of the initially more frequent allele.

Figure 3



Dynamics of the genotypic frequencies for homotypic mating predisposition and mating equivalence of the two homozygous genotypes; the sexual specific degrees of homotypic predisposition are $\alpha_{FHo} = 0.2,\ \alpha_{F12} = 0.3,\ \alpha_{MHo} = 0.8$ *and* $\alpha_{M12} = 0.7$.

This observation can be explained as follows: According to equation (8.3), for polymorphic equilibrium states outside the range $q_1 = q_2$, the mating success must be identical for the two types, i.e. $h_{Ho} = h_{12} = 1$. Because of the positive frequency dependence of the mating success, there exists exactly one value for Q_{Ho} ($:= \hat{Q}_{Ho} = 1 - \hat{Q}_{12}$) satisfying this equation, and, since $h^*_{Ho} < 1$, the inequality $\hat{Q}_{12} < \frac{1}{2}$ must hold. Moreover, for fixed $\hat{Q}_{Ho}$ all mating frequencies are invariant, so that, according to equation (8.4), the transition from $Q_{12} = \hat{Q}_{12}$ to Q'_{12} in the next generation exclusively depends upon the absolute value of the difference $Q_{11} - Q_{22}$, where this value can vary between the bounds set by 0 and $\hat{Q}_{Ho}$. Thus, in particular, $Q_{11} = Q_{22}$ implies $Q'_{12} > \hat{Q}_{12}$, and $Q_{11} = 0$ or $Q_{22} = 0$ implies $Q'_{12} = \frac{1}{2}(1 - P(T_{Ho} \times T_{Ho})) < \frac{1}{2} \cdot (2h_{12}\hat{Q}_{12}) = \hat{Q}_{12}$. Consequently, one obtains for Q_{11} (or Q_{22}) exactly two symmetrically located values $Q_{11} = \hat{Q}_{11}$, each of which implies $Q'_{12} = \hat{Q}_{12}$. This corroborates the impression given by the graphical representation, namely that there exist two additional polymorphic equilibria. Clearly, because of their symmetry, these equilibria cannot be distinguished on the level of the phenotypes: they are phenotypically cryptic.

It is obvious that, beyond the present special case, this method of proving the existence of additional polymorphic genotypic equilibria applies to all situations in which the difference in mating success of the two types is a strictly monotone (increasing or decreasing) function of Q_{Ho}, and where the mating frequencies depend solely on the relative frequencies of the two types. This fact will be taken advantage of in the next subsection, where effects of negative frequency dependence on the dynamics of the genotypic frequencies will be studied for heterotypic mating predisposition.

Heterotypic mating predisposition: Following the same pattern as in the last subsection, one obtains from the equations (7.10) for the mating frequencies with heterotypic mating predisposition:

$$P(T_{Ho} \times T_{Ho}) = \frac{(1-\alpha_{FHo})(1-\alpha_{MHo})}{1-\alpha_{MHo}\cdot Q_{Ho}} \cdot Q_{Ho}^2 \ ,$$

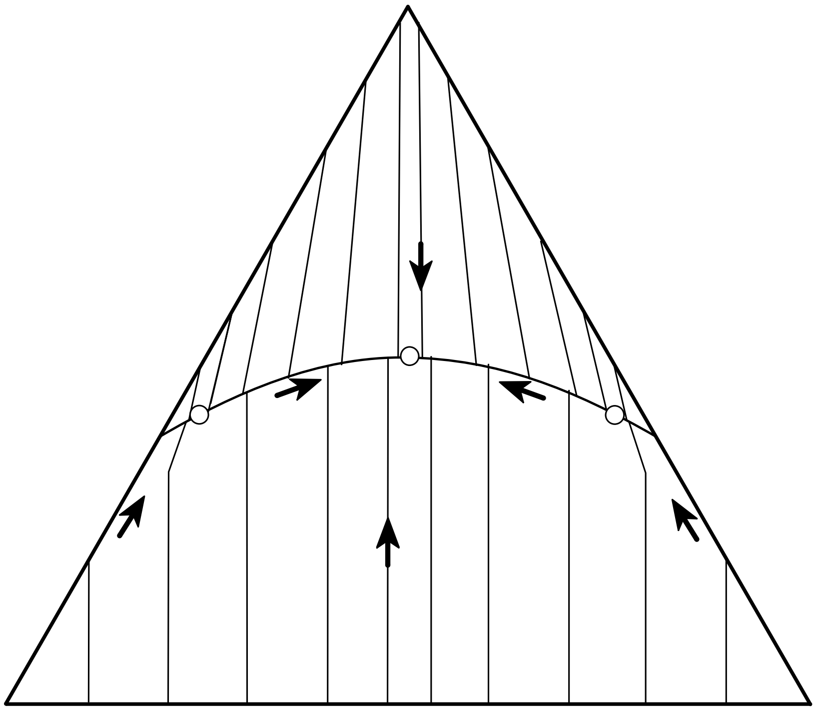
$$\begin{aligned} P(T_{Ho}) =& \frac{1}{2}\cdot\frac{1-Q_{12}(1-\alpha_{F12})}{1-Q_{12}}\cdot Q_{Ho} + \frac{1}{2}\cdot\frac{1-\alpha_{F12}}{1-\alpha_{M12}Q_{12}}\cdot Q_{Ho}Q_{12} + \\ &+ \frac{1}{2}\cdot\frac{(1-\alpha_{FHo})(1-\alpha_{MHo})}{1-\alpha_{MHo}Q_{Ho}}\cdot Q_{Ho}^2 \ . \end{aligned}$$

For negative frequency dependence in mating success of the two types relative to each other (which is the only interesting ranking of mating success in the present model), dynamics deviating from global convergence to the central equilibrium can be expected to occur only if for equal frequency of the two types ($Q_{Ho} = Q_{12} = \frac{1}{2}$) the mating success of the homozygous type (again denoted by h^*_{Ho}) fulfills the condition $h^*_{Ho} > 1$. From the above equation, one obtains

$$2\cdot(h^*_{Ho}-1) = \frac{1-\alpha_{MHo}}{2-\alpha_{MHo}}\cdot(1-\alpha_{FHo}) - \frac{1-\alpha_{M12}}{2-\alpha_{M12}}\cdot(1-\alpha_{F12}) \ ,$$

so that $h^*_{Ho} > 1$ is realized if, for example, one of the following conditions holds true: (1) $\alpha_{MHo} < \alpha_{M12}$ and $\alpha_{FHo} < \alpha_{F12}$; (2) $\alpha_{M12} = \alpha_{MHo} < 1$ and $\alpha_{FHo} < \alpha_{F12}$; or (3) $\alpha_{F12} = \alpha_{FHo} < 1$ and $\alpha_{MHo} < \alpha_{M12}$.

Figure 4



Dynamics of the genotypic frequencies for frequency dependent realization of heterotypic mating predisposition and mating equivalence of the two homozygous genotypes; $n_{Ho} = 1,\ n_{12} = 2$.

However, as was emphasized in section 7.2, the assumption of constant degrees of heterotypic mating predisposition is only of limited biological significance. Therefore, the following analysis will concentrate on the model of frequency dependent realization of mating predispositions which exist only in the female sex. Moreover, a saturation phase will not be considered, so that the parameters of heterotypic mating predisposition are characterized by $\alpha_{MHo} = \alpha_{M12} = 0,\ \alpha_{FHo} = 1 - Q_{Ho}^{n_{Ho}}$ and $\alpha_{F12} = 1 - Q_{12}^{n_{12}}$. Recall that the parameter n specifies the number of encounters over which a female individual maintains its heterotypic mating predisposition. Hence, the assumption $h_{Ho}^{*} > 1$ can be realized only under the above condition (2), which implies $n_{Ho} < n_{12}$. Figure 4 illustrates the dynamics of the genotypic frequencies under this condition for the parameter n for several initial frequencies.

Apparently, in addition to the central equilibrium, there again exist two symmetrically located polymorphic equilibrium states. However, as opposed to homotypic predisposition, these equilibria are locally attractive, and the central equilibrium is repelling. The formal proof for the existence of the symmetrical equilibria is exactly the same as in the last subsection on homotypic predisposition. Thus, with respect to the existence of additional polymorphic equilibrium states, homotypic and heterotypic mating predisposition are quite similar, but, in accordance with the different modes of frequency dependence of the mating success predominating in the two mating systems, these equilibrium states play opposite roles.

<<<<<<<<<>>>>>>>>>

Summarizing the results of the present chapter, it can be emphasized that the mode of inheritance of an observable phenotypic variation may confer an at least limited evolutionary advantage even to such types that are at a reproductive disadvantage (in the sense of mating success). Even though in all of the models treated above, the reproductively superior type did not asymptotically disappear from the population (was protected), this should not be generalized without restrictions. For example, if one abandons the assumption of regular segregation and allows for arbitrary forms and degrees of segregation distortion, even a globally reproductively superior type may be displaced from the population. Such situations can even be realized in cases as simple as complete dominance of one of the two alleles at a diploid gene locus over the other.

9. Heterophasic mating (gametophytic incompatibility)

In essence, the term **gametophytic incompatibility** refers to situations where the mating compatibility depends on characteristics of the diplophase for one partner and on characteristics of the haplophase for the other partner. As a rule, the characteristics of the diplophase refer to the producers of female gametes while the characteristics of the haplophase refer to male gametes themselves (not their producers). This marks a fundamental difference from all of the systems treated so far in the special models, since in these models both mating partners were characterized with respect to the same phase, mainly the diplophase. In order to distinguish systems where mating events are considered for pairs of individuals characterized by the same phase (both partners are either referred to the diplophase, which includes sporophytic incompatibility, or both are referred to the haplophase) from gametophytic incompatibility, they will be termed systems of **homophasic mating**. Moreover, since the term “gametophytic incompatibility” is commonly used in a more restricted sense than described above, it is advisable to introduce **heterophasic mating** as the counterpart of homophasic mating in the sense that the two partners involved in a mating event are characterized with respect to different phases (one with respect to the diplo- and the other with respect to the haplophase). Note that the general typification and definition of mating events used for the characterization of mating systems in the present treatise also account for the possibility of heterophasic mating.

These two terms must not be confused with the levels at which mating events are defined. For both homophasic and heterophasic mating, the mating event can, for example, be defined on the level of the haplophase by the fusion of gametes. If, furthermore, the typification of the gametes is carried out such that each gamete is assigned the type of its producer (belonging to the diplophase) without any additional reference to characteristics of the gamete itself, then a system of homophasic mating is addressed which is oriented at the diplophase (see sections 3.1 and 3.2). On the other hand, retaining the definition of the mating event as the fusion of gametes, a system has to be classified as heterophasic mating, if, for example, each female gamete is typified solely by characteristics of its producer (diplophase) while the typification of each male gamete solely depends on its own (haplophase) characteristics.

Gametophytic incompatibility is primarily realized in angiosperms, since the more complex processes of fertilization involving, for example, germination of the pollen on the stigma and pollen tube growth in the style provide many possibilities for interaction between components of the diplophase (stigma, style) and of the haplophase (pollen). These interactions, as far as observable, are in most cases of a primarily genetic nature and are therefore classified into "homogenic" and "heterogenic" forms of incompatibility. **Homogenic incompatibility** is known to occur frequently in angiosperms as systems of self-sterility genes. In these systems, fertilization is impeded or even completely prevented if a pollen grain carries a gene that is also present in the producer of the ovule (as applies to many cabbage species, geranium, rye, or coffee). As a consequence, the possibilities for self-fertilization are reduced. Similar consequences are implied by heterostyly, as can be found, for example, in several primrose species, forsythia, narcissus, or purple loosestrife. **Heterogenic incompatibility** has the opposite effect in that fertilization (as well as the preceding processes) is (are) impeded between carriers of different genes. However, this system of (cross-) incompatibility appears to be known only for fungi. Both systems of incompatibility are based on the concept that the possibilities for mating are determined by genetic similarity relationships between the mating partners, so that homogenic and heterogenic incompatibility can be classified as systems of heterotypic and homotypic mating predisposition in the sense introduced in section 7.2. These correspond in turn to negative and positive assortative mating, respectively.

A generalized characterization of gametophytic incompatibility as systems of heterophasic mating should, however, also allow for situations in which at least some of the above-mentioned phenomena cannot be unambiguously observed. Perhaps such a generalization will lead to concepts that reflect the biological reality more closely than do the frequently applied, restricted characterizations. In particular, the notion that incompatibility ought to prevent successful fertilization in each case is debatable. It may be true that, when compatible and incompatible pollen are simultaneously present on a stigma, all ovules are fertilized exclusively by the compatible pollen types. Yet, full seed set can also be obtained for exclusive pollination with incompatible pollen if, for example, incompatibility entails a retardation but not cessation of pollen tube growth. In this case all ovules would be fertilized by incompatible pollen, since it would not have to compete with the compatible type. In other words, incompatibility relationships need not in all cases be strict but may rather vary in degree according to the frequencies of the incompatibility and compatibility types (for a review and special examples see e.g. Steiner 1988). It is thus again meaningful to aim at a generalized representation in terms of mating preferences and to use these preferences for the interpretation and classification of different concrete systems of incompatibility.

General representation

As follows from the above definition, in systems of heterophasic mating the set of potential mating partners can basically be divided into two groups. One group consists of all individuals that affect the mating process via characteristics of the diplophase (e.g. the producers of female gametes). The typification in this group will be distinguished by the notation T_{Di}, where the subscript D indicates the diplophase. The other group is characterized by traits of the haplophase and thus consists, for example, of all male gametes; the notation T_{Hj} will be used for the typification of individuals (male gametes) belonging to this group. Thus, a mating event of the type $T_{Di} \times T_{Hj}$ describes the fusion of a female gamete produced by a T_{Di}-individual with a male gamete of type T_{Hj}. So far, no formal distinction can be made between heterophasic mating and homophasic mating in a dioecious population, since the subscripts D and H simply have to be replaced by F and M, respectively, to arrive at the representation of dioecious populations. Since the typifications indexed by F and D both refer to the same object, namely the producers of female gametes, the identification $T_{Fi} = T_{Di}$ is justifiable. However, with respect to the subscripts M and H this would be meaningless, even though both T_{Mj} and T_{Hj} refer to male gametes, since, while T_{Mj} is identical for the gamete and its producer, T_{Hj} makes no reference at all to the producer of the gametic type indicated and thus cannot be used as a simultaneous characterization of the two phases.

A clear distinction between heterophasic and homophasic mating is essential in all experimental studies, where the mating event is defined by the fusion of gametes, the mating type is identified in the zygotes or other early stages of the life cycle with the help of genetic techniques, and where the female but not the male parent of the offspring is known. For many organisms (particularly for gymnosperms with their haploid endosperms), it is then possible to distinguish genetically between the female and the male gametic contribution to the offspring (seed, in the case of gymnosperms). Consequently, the successful female gamete can be assigned the type of its producer, while the possibilities for typification of the successful male gamete are restricted to its haplogenotype and cannot incorporate any characteristics of its producer. Since the female parents are known in any case, they can be scored for arbitrary traits (not just those dictated by the genetic techniques applied), and the resulting typification can be used for the specification of the distribution of potential female mating partners for the male gametes. On the other hand, the possibilities for typification of the male gametes are limited by the genetic techniques applied, and information on the frequency distribution of haplogenotypes in the total male gametic output of a population is difficult to obtain. Hence, mating references for the female parents will usually be based on estimates derived from the (diplo-) genotypic frequencies among the potential producers of male gametes. This situation is typical of many experimental genetic studies of mating systems in animal or plant populations and is thus suitable for the characterization of systems of heterophasic, but not of homophasic, mating.

These last explanations emphasize once more that the notion of gametophytic incompatibility, which is usually applied only to angiosperms, finds its appropriate generalization in the concept of heterophasic mating, which, in turn, simplifies the identification of related incompatibility systems in other systematic categories. However, some important and general characteristics of heterophasic mating can already be demonstrated with the help of models, the formulation of which is guided along mechanisms of gametophytic incompatibility in angiosperms. The model to be introduced in the following section traces back to an idea of M.D. Ross (personal communication, see also the work of Steiner cited above).

9.1 Differential pollen tube growth

The majority of the results from experimental studies of gametophytic incompatibility directly reveal or can be explained by the property of particular pollen types to germinate slowly or not at all on the stigmata of particular plants and/or to show retarded pollen tube growth in the style, which can possibly even come to a complete halt before reaching the ovule. These phenomena can be collected under the term “differential pollen tube growth”, and their analysis must be based on a comparison between the composition of the pollen on the stigma and the composition of the pollen after they become successful in fertilization. Hence, according to the present terminology, the mating reference of an individual or type in the diplophase is specified by the pollen that arrives at its stigmata. Other mating references considering, for example, the composition of the pollen production prior to its distribution to the stigmata are not suitable, since they may introduce influences obscuring the specific effects of differential pollen tube growth. In order to include the possibility for individual self-pollination, the mating references $R_{Hj \triangleleft Di}$ of the diplophase must be divided into individual self-mating and cross-mating references. The fact that pollen involved in self-pollination may differ in type explains the necessity of self-mating references (such references are not required for homophasic mating). The following notation will be used for the different mating references and the quantities specifying the relationships between them:

Notations

$R^c_{Hj \triangleleft Di}$:= cross-mating reference of T_{Di}-individuals, i.e. the proportion of T_{Hj}-pollen among all pollen cross-pollinating T_{Di}-stigmata.

$R^s_{Hj \triangleleft Di}$:= self-mating reference of T_{Di}-individuals, i.e. the proportion of T_{Hj}-pollen among all pollen originating from individual self-pollination of T_{Di}-stigmata.

s_i := the proportion of individual self-pollination among all pollen which arrived at T_{Di}-stigmata.

$R_{Hj \triangleleft Di}$:= mating reference of T_{Di}-individuals, i.e. the proportion of T_{Hj}-pollen among all pollen which arrived at T_{Di}-stigmata.

The self- and cross-mating references yield the overall mating reference according to the equation

$$R_{Hj \triangleleft Di} = s_i \cdot R^s_{Hj \triangleleft Di} + (1 - s_i) \cdot R^c_{Hj \triangleleft Di} \ . \tag{9.1}$$

Under the assumption of random cross-pollination, all diplophase types (T_{Di}) have the same cross-mating references, so that $R^c_{Hj \triangleleft Di} = R^c_{Hj}$ for all i and j. With the exception of extreme cases, identical self-mating references for all diplophase types cannot be realized, since, as a rule, the compositions of the pollen production of the various diplophase types may differ substantially.

In order to be able to classify differential pollen tube growth as a system of gametophytic incompatibility, it is indispensable to measure the speed of growth of the pollen tubes in the pistils by its result, namely differential fertilization success. It is obvious that fertilization success is also influenced by factors that are not directly associated with pollen tube growth, such as differential timing in maturity or distribution of the pollen. However, all these factors are in effect equivalent to differential pollen tube growth and can thus be meaningfully summarized under this term.

It is therefore justified to proceed from the simplifying assumption that all pollen grains arrive at stigmata at the same time, so that they are subject to identical initial conditions. The competition of two pollen grains for fertilization of an ovule would thus be won by the faster growing pollen. It would in this context be irrelevant to quantify the difference in speed of growth. Consequently, since the distribution of the pollen over the stigmata includes random effects to some extent, an appropriate measurement of differences in growth between pollen types ought to be carried out in terms of the proportions with which they fertilize the ovules. The proportions of the pollen types before and after fertilization are given by the mating references $R_{Hj \lhd Di}$ and the mating norms $P_{Hj \lhd Di}$, respectively. Hence, the fraction of fertilizing pollen among all T_{Hj}-pollen which arrived at T_{Di}-stigmata is proportional to $P_{Hj \lhd Di}/R_{Hj \lhd Di}$. This quotient, however, happens to be the mating preference $U_{Hj \lhd Di}$ of T_{Di}-individuals for T_{Hj}-pollen. Superiority in pollen tube growth of one pollen type over another in a given pistil type thus becomes manifest in greater mating preference by this pistil type. The efficiency in pollen tube growth of two types relative to one another can be evaluated by a comparison of their preferences by the pistil type.

Result

The statement "T_{Hj}-pollen grow faster in T_{Di}-pistils than do T_{Hk}-pollen" is equivalent to $U_{Hj \lhd Di} > U_{Hk \lhd Di}$. With respect to the efficiency in fertilization of the ovules in T_{Di}-pistils the difference in speed of growth between the two pollen types is irrelevant; in effect, it is rather the quotient $U_{Hj \lhd Di}/U_{Hk \lhd Di}$ that appropriately measures the superiority in pollen tube growth.

Having demonstrated that the efficiency of pollen tube growth is appropriately measured by the mating preferences, it is now possible to classify and quantify the different forms of pollen tube growth solely in terms of mating systems. For example, if on the average each pollen type has the same speed of growth in T_{Di}-pistils, then this is equivalent to random mating of T_{Di}-individuals with all of their potential mating partners (the pollen types on their stigmata; $U_{Hj \triangleleft Di} = 1$ for all j). On the other hand, if only certain pollen types, those belonging to a set $\mathcal{H}$, say, show the same speed of growth, conditional random mating in the sense of section 1.4 is realized, and all pollen types T_{Hj} belonging to the set $\mathcal{H}$ ($j \in \mathcal{H}$) are equally preferred in the matings of T_{Di}-individuals.

In particular, the assumption of conditional random mating allows division of the pollen types arriving at a stigma type into two disjoint sets reflecting the dichotomous view of fast and slowly growing pollen. Thus, one set would comprise all pollen types considered to be fast growing, and its complement would consist of those types considered to grow more slowly. Clearly, in order to maintain this view, it has to be assumed that within each of the two sets no substantial differences between the types in speed of pollen tube growth exist. The sets of fast and slowly growing pollen types may differ in composition between the pistil types. Although this reduction in complexity can only be accepted as an approximation to real situations, it helps to elaborate some important features of differential pollen tube growth with the help of simple models which are nevertheless clearly in line with basic biological facts. The following subsection presents such a model.

A MODEL

The formulation of the model is based on angiospermous species in which *each pistil harbors only one egg cell*, so that the pollen grains arriving at a stigma compete for just one egg cell. As explained above, it will be assumed that for each pistil type the arriving pollen types can be divided into fast and slowly growing types. The symbols specified in the following Table of notations will be used for the further specification of the model.

Notations

$N_i :=$ the average number of pollen grains arriving at a stigma of type T_{Di} (**pollination density** on this stigma type);

$\mathcal{H}_i :=$ the set of pollen types which grow fast in T_{Di}-pistils; hence, a pollen type T_{Hj} grows fast in T_{Di}-pistils if $j \in \mathcal{H}_i$. The pollen type is classified as slowly growing in these pistils if $j \notin \mathcal{H}_i$. All pollen types belonging to $\mathcal{H}_i$ are assumed to have largely the same speed of growth, and this is also assumed to hold for all pollen types not belonging to $\mathcal{H}_i$.

It has come into use to refer to the set $\mathcal{H}_i$ as pollen types "compatible" with T_{Di}-pistils (stigmata, styles); the types not represented in this set are thus the "incompatible" pollen types. This terminology is somehow unfortunate, since it may give the impression that under all circumstances only the "compatible" pollen types are capable of fertilizing the ovules. As was pointed out in the introduction to the present chapter, this concept is probably unfounded in many if not the majority of cases: fertilization can also occur with "incompatible" pollen if "compatible" pollen types are absent or sufficiently rare.

- ▷ *Mode of fertilization:* The last remark gives rise to the assumption, which is central for the present model, that an ovule is always fertilized by the faster growing pollen types if they were represented by at least one pollen grain among the pollen which arrived at the respective stigma. If only the slowly growing types were represented, then the ovule is fertilized by one of these types. This assumption reflects the advantage in competition of faster pollen tube growth, and it implies that an ovule is always fertilized if, irrespective of its type, at least one pollen grain arrives at its stigma.
- ▷ *Mode of pollination:* It remains to specify the mode according to which (and based on the mating references given in equation (9.1)) the pollen is distributed over the single stigmas. In this connection, two aspects have to be taken into account. One concerns the distribution of the total number of pollen grains arriving at a stigma, and the second is concerned with the frequency distribution of the pollen types among all pollen that arrived at the stigma. Since the overall pollen production

of the population can be assumed to be very large, the total number of pollen grains can be postulated to follow a Poisson distribution with parameter N_i for T_{Di}-stigmata. For any given number of pollen grains which arrive at a stigma type, the frequencies of the various pollen types are postulated to follow a multinomial distribution with parameters given by the mating references in equation (9.1). This reduces to a binomial distribution if all types growing fast in T_{Di}-pistils are collected under one type $\mathcal{H}_i$.

Mating norms: According to the Poisson distribution, the probability that n pollen grains arrive at a T_{Di}-stigma is given by $e^{-N_i} \cdot N_i^n/n!$. Moreover, among these n pollen grains the frequency of fast growing types is binomially distributed, where the frequency of fast growing pollen types on all T_{Di}-stigmata is given by the sum $\lambda_i := \sum_{j\in\mathcal{H}_i} R_{Hj\triangleleft Di}$ over the respective mating references. Hence, the probability of finding k fast growing pollen grains among n pollen grains that arrived at a T_{Di}-stigma is equal to $\binom{n}{k}\lambda_i^k(1-\lambda_i)^{n-k}$. Since n is a Poisson-distributed random variable, the unconditional probability of finding k pollen grains on a T_{Di}-stigma that are fast growing in the pertinent pistil is $e^{-N_i\lambda_i} \cdot (N_i\lambda_i)^k/k!$. This again represents a Poisson distribution with the parameter now given by the average number $N_i \cdot \lambda_i$ of pollen grains that arrive on T_{Di}-stigmata and are fast growing in the pertinent pistils. The central parameters involved in these distributions (in addition to those defined earlier) are thus:

Notations

$\lambda_i :=$ $\sum_{j\in\mathcal{H}_i} R_{Hj\triangleleft Di}$, or relative frequency of pollen grains that are fast growing in T_{Di}-pistils among all pollen grains which arrived at the pertinent stigmata;

$N_i \cdot \lambda_i :=$ average number of pollen grains that arrive at T_{Di}-stigmata and are fast growing in the pertinent pistils.

Equating in the expression $e^{-N_i}N_i^n/n!$ the number n of pollen grains to 0, one arrives at the probability e^{-N_i} of a T_{Di}-ovule not to be fertilized. Hence, the fraction of fertilized ovules among all T_{Di}-ovules is $1 - e^{-N_i}$. Furthermore, the probability of a T_{Di}-ovule to be fertilized by pollen that is fast growing in the pertinent pistil is equal to the probability that at least one such pollen grain arrives at a T_{Di}-stigma. Hence, applying the compound Poisson distribution, one computes this probability to be

$$1 - e^{-N_i \lambda_i}.$$

Among all fertilized T_{Di}-ovules (the fraction of which is $1 - e^{-N_i}$), a fraction $(1 - e^{-N_i\lambda_i})/(1 - e^{-N_i})$ derives from fertilizations with fast growing pollen. Because of the equivalence of all fast growing pollen types, random preferential mating (see section 1.4) of T_{Di}-ovules takes place with all pollen types belonging to $\mathcal{H}_i$. Hence, among these matings, pollen of type T_{Hj} ($j \in \mathcal{H}_i$) has a share of $R_{Hj \lhd Di}/\lambda_i$. Analogously, the fraction of slowly growing pollen among all fertilizations of T_{Di}-ovules is $(e^{-N_i\lambda_i} - e^{-N_i})/(1 - e^{-N_i})$, and from this, in turn, a fraction $R_{Hj \lhd Di}/(1 - \lambda_i)$ is due to pollen of type T_{Hj} ($j \notin \mathcal{H}_i$). In summary, one thus derives the mating norm of T_{Di}-individuals to be

$$P_{Hj \lhd Di} = \begin{cases} \dfrac{1 - e^{-N_i\lambda_i}}{1 - e^{-N_i}} \cdot \dfrac{R_{Hj \lhd Di}}{\lambda_i} & \text{for } j \in \mathcal{H}_i \\[2ex] \dfrac{e^{-N_i\lambda_i} - e^{-N_i}}{1 - e^{-N_i}} \cdot \dfrac{R_{Hj \lhd Di}}{1 - \lambda_i} & \text{for } j \notin \mathcal{H}_i . \end{cases} \tag{9.2}$$

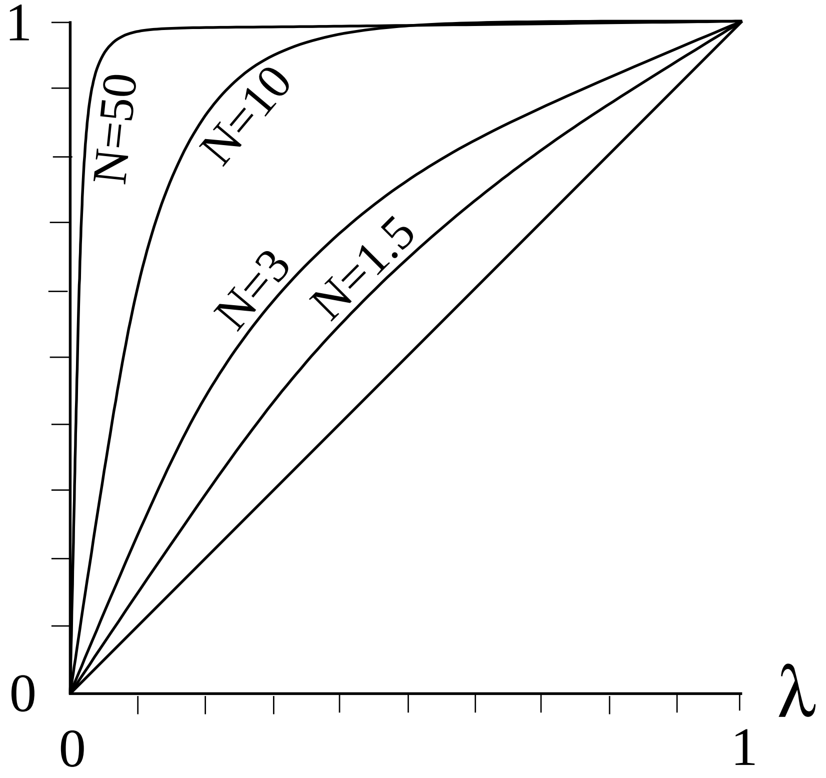
In particular, fast growing pollen types are involved in the proportion $P_{\mathcal{H}_i \lhd Di} = \sum_{j \in \mathcal{H}_i} P_{Hj \lhd Di}$ among all matings of T_{Di}-individuals. Hence, by the above equation (9.2)

$$P_{\mathcal{H}_i \lhd Di} = \frac{1 - e^{-N_i\lambda_i}}{1 - e^{-N_i}} \; . \tag{9.3}$$

This frequency is a monotone increasing and concave function of λ_i and thus of the fraction of fast growing pollen among the potential mating partners of T_{Di}-individuals. Figure 5 illustrates this fact for several average pollination densities N_i of T_{Di}-stigmata. It is remarkable that, for high pollination densities N_i, a very small frequency of fast growing pollen types on the stigmata (λ_i close to 0) is already sufficient to guarantee that almost all ovules are fertilized by these pollen types.

Mating preferences: The last remark hints at the possibility for extremely large mating preferences for fast growing pollen types, provided they are rare on the stigmata. To verify this, consider the mating preferences of T_{Di}-individuals, which can be immediately derived from equation (9.2):

Figure 5

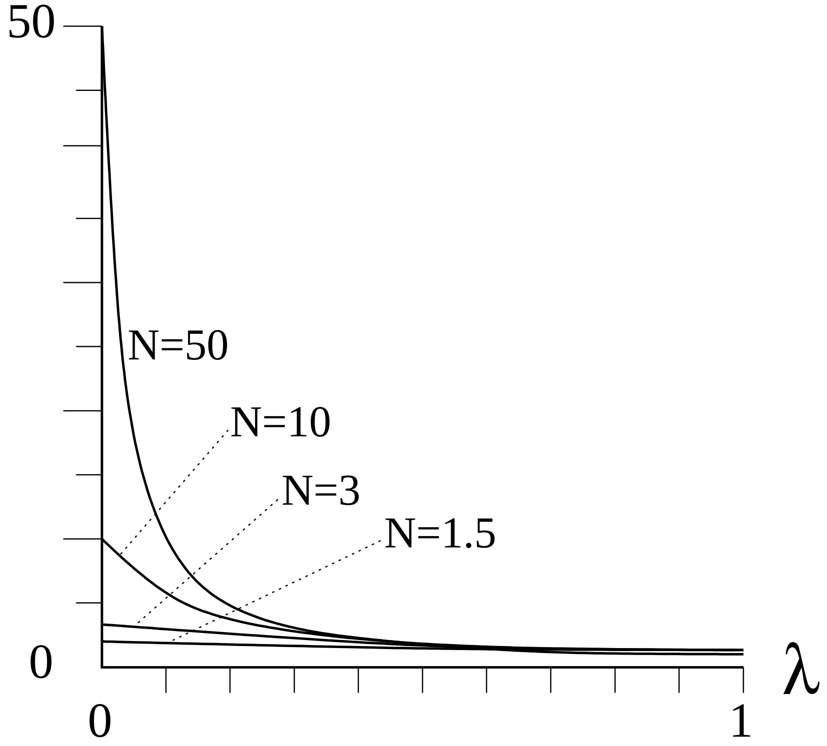


Probability of fertilization of an ovule by fast growing pollen types as a function of their average frequency λ on the stigmata. N denotes the pollination density on a given stigma type (average number of pollen grains arriving on a stigma).

$$U_{Hj\lhd Di} = \begin{cases} \dfrac{1-e^{-N_i\lambda_i}}{\lambda_i(1-e^{-N_i})} & \text{for } j \in \mathcal{H}_i \\ \dfrac{e^{-N_i\lambda_i}-e^{-N_i}}{(1-\lambda_i)(1-e^{-N_i})} & \text{for } j \notin \mathcal{H}_i. \end{cases} \tag{9.4}$$

As a consequence of conditional random mating, all mating preferences for fast growing pollen types are identical, and the same is true for all slowly growing pollen types. As was to be expected, the mating preferences $U_{\mathcal{H}_i\lhd Di}$ for fast growing pollen types are greater than 1, and they are monotone decreasing and convex functions of λ_i. With the help of the rule of de l'Hospital, it is shown that for $\lambda_i \to 0$, $U_{\mathcal{H}_i\lhd Di}$ ($= U_{Hj\lhd Di}$ for all $j \in \mathcal{H}_i$) approaches its upper limit $N_i/(1-e^{-N_i})$. This confirms the above-stated expectation that high mating preferences for fast growing pollen types can be realized if the latter are rare on the stigmata and the pollination density is high. On the other hand, since $U_{\mathcal{H}_i \triangleleft Di} < 1/\lambda_i$ always holds, the preference for fast growing pollen types must decrease rapidly with increasing frequency of these pollen types on the stigmata. These phenomena are illustrated in Figure 6.

Figure 6



Mating preference for fast growing pollen types as a function of their average frequency λ on the stigmata. N denotes the pollination density on a given stigma type.

As was shown above, an appropriate measure of the degree of superiority in pollen tube growth of fast relative to slowly growing pollen types is provided by the quotient of the respective mating preferences by a given pistil type. According to equation (9.4), this quotient of the two mating preferences by T_{Di}-individuals is given by

$$\frac{(1 - e^{-N_i\lambda_i}) \cdot (1 - \lambda_i)}{(e^{-N_i\lambda_i} - e^{-N_i}) \cdot \lambda_i} \ ,$$

which is a monotone increasing function of λ_i with lower bound $N_i/(1 - e^{-N_i})$ and upper bound $(e^{N_i} - 1)/N_i$. Hence, particularly for large pollination density on T_{Di}-stigmata, the fertilization efficiency of the fast growing pollen types is always considerably higher than that of the slowly growing types. If, in addition, the slowly growing types are rare on the stigmata, the mating preference by the pertinent pistil type may become so small that the above quotient may reach extremely large values. For example, given a pollination density of $N_i = 10$ pollen grains per T_{Di}-stigma, the efficiency in fertilization of the fast growing pollen types is at least 2000 times that of the slowly growing types. Even if the slowly growing pollen types were very frequent on the stigmata, the fast growing types were still at least 10 times as efficient in fertilization of the ovules. The most important characteristics of the present model can thus be summarized as follows:

Result

For a given pistil type, its mating preferences for fast growing pollen types are greater than 1. These mating preferences increase rapidly with decreasing frequency of the fast growing pollen types on the pertinent stigmata, and they can reach very large absolute values for high pollination density of the stigmata. The latter is a consequence of the fact that the mating preference of the pistil type for fast growing pollen types increases with the pollination density of its stigmata.

Mating frequencies: As was shown above, the probability for fertilization of an ovule depends on the pollination density of its pertinent stigma, which was derived to be $1 - e^{-N_i}$ for T_{Di}-ovules with pollination density N_i. However, on the average, it needs just $N_i \geq 4.7$ pollen grains to fertilize more than 99% of the ovules in T_{Di}-pistils. Consequently, only for comparatively low average pollination density of the stigmata is it necessary to take account of the possibility that not all ovules are fertilized.

Now, let Q_i^D be the relative frequency of T_{Di}-ovules among all ovules in the population (which is identical to the relative frequency of T_{Di}-individuals if all types produce the same number of ovules). Then

$$P(T_{Di}) = \frac{\frac{1}{2}(1 - e^{-N_i}) \cdot Q_i^D}{\sum_k (1 - e^{-N_k}) \cdot Q_k^D} \ .$$

From this the mating frequencies are obtained by applying equation (1.1) to equation (9.2):

$$P(T_{Di} \times T_{Hj}) = \begin{cases} \dfrac{(1 - e^{-N_i\lambda_i}) \cdot Q_i^D}{1 - \sum_k Q_k^D e^{-N_k}} \cdot \dfrac{R_{Hj \triangleleft Di}}{\lambda_i} & \text{for } j \in \mathcal{H}_i \\ \dfrac{(e^{-N_i\lambda_i} - e^{-N_i}) \cdot Q_i^D}{1 - \sum_k Q_k^D e^{-N_k}} \cdot \dfrac{R_{Hj \triangleleft Di}}{1 - \lambda_i} & \text{for } j \notin \mathcal{H}_i . \end{cases} \tag{9.5}$$

These equations form the basis on which conditions for the evolution of differential pollen tube growth will be analyzed in the next section. Consequently, the main emphasis will be put on the characterization of the compatibility relationships between pistil types and pollen types that can help to explain the stable coexistence of pollen types showing differential speed in pollen tube growth.

9.2 Evolution of differential pollen tube growth

Having become familiar with the fact that different modes of inheritance considered for the same phenotypes may have different effects on the quality and quantity of the evolutionary dynamics of these phenotypes, it is logically consistent to again start with the simplest mode of inheritance of differential pollen tube growth (in the generalized sense of section 9.1), namely a single, diploid, autosomal gene locus with alleles $A_1, A_2, \ldots, A_n$. In its diploid state (in the diplophase), this gene locus is assumed to determine interacting characteristics of both the pistils and, in the haploid state, the pollen. Thus, with respect to differential pollen tube growth, the types of the diplophase (pistils) are represented by the $n(n+1)/2$ genotypes A_iA_j $(i, j = 1, \ldots, n)$, and the types of the haplophase (pollen) are represented by the n alleles $A_1, \ldots, A_n$. Since there is no danger of ambiguity, the types of the diplophase will be indexed by ij in place of Dij, and, similarly, for the haplophase the subscript i will be taken to replace Hi. For the same reason, the relative frequencies Q_{ij}^D of the genotypes A_iA_j will be replaced by Q_{ij}. Moreover, $q_i = \sum_j \frac{1}{2}(1 + \delta_{ij})Q_{ij}$ will denote the relative frequency of the allele A_i in the diplophase.

In order to exclude selective effects that differ in nature from those directly emanating from differential pollen tube growth, some restrictive assumptions are necessary. The most obvious assumption is that the ovules do not contribute to differential mating success, which requires that

(i) all ovule types have the same probability to be fertilized, and regular segregation of the alleles is realized among the ovules.

It follows immediately from this assumption that

$$2 \cdot P(T_{ij}) = Q_{ij} \quad \text{for all } i, j,$$

which, together with the assumption of regular segregation, allows the transition equations for the genotypic frequencies Q_{ij} in the diplophase to be written in the form

$$\begin{aligned} Q'_{ii} &= \sum_k \tfrac{1}{2}(1+\delta_{ik}) P_{i \triangleleft ik} Q_{ik}, \\ Q'_{ij} &= \sum_k \tfrac{1}{2}(1+\delta_{ik}) P_{j \triangleleft ik} Q_{ik} + \sum_k \tfrac{1}{2}(1+\delta_{jk}) P_{i \triangleleft jk} Q_{jk} \quad \text{for } i \neq j, \\ q'_i &= \tfrac{1}{2} q_i + \tfrac{1}{2} \sum_{j \le k} P_{i \triangleleft jk} Q_{jk}. \end{aligned} \tag{9.6}$$

Note that the last summand in the transition equation for the allele frequencies is actually the frequency $P(T_i)$ with which A_i-pollen participate in the matings. Moreover, on the side of the pollen, the mating references given in equation (9.1) must be specified such that they do not per se entail differential mating success:

(*ii*) among the pollen produced, regular segregation is realized;
(*iii*) the proportions of individual self-pollination are identical for all genotypes, i.e. $s_{ij} \equiv s$;
(*iv*) the cross-mating references of the types of the diplophase are given by the frequencies of the alleles in the diplophase, i.e. $R^c_{i \triangleleft jk} = q_i$.

Assumption (*ii*) excludes segregation distortion among the pollen as a potential factor of allelic selection taking place prior to mating. Assumption (*iii*) guarantees that a genotype of the diplophase cannot increase its chance to become successful in the mating process via its pollen by a larger amount of individual self-pollination (see also section 5.3 and the introduction to chapter 6). Finally, assumption (*iv*) makes sure that all genotypes of the diplophase contribute equally to the cross-pollination of all stigma types, as is the case, for example, for identical pollen fertilities of all genotypes and random cross-pollination. Considering that, according to assumption (*ii*), the self-mating references are given by $R^s_{i \triangleleft jk} = \frac{1}{2}(\delta_{ij} + \delta_{ik})$, the overall mating reference given in equation (9.1) turns out to be

$$R_{i \triangleleft jk} = \tfrac{1}{2}(\delta_{ij} + \delta_{ik}) \cdot s + (1-s) \cdot q_i \ . \tag{9.7}$$

The mating preferences based on these references are now $U_{i\triangleleft jk} = P_{i\triangleleft jk}/R_{i\triangleleft jk}$. The significance of these mating preferences for the evolutionary dynamics can be demonstrated in a very clear manner by assuming that A_i-pollen shows above average pollen tube growth in all pistil types, so that $U_{i\triangleleft jk} > 1$ and thus $P_{i\triangleleft jk} > R_{i\triangleleft jk}$ holds for all j and k. Applying this inequality to the transition equation (9.6) for the allele frequencies and inserting the mating references (9.7), one obtains $q_i' > q_i$. Hence, for arbitrary initial frequencies, allele A_i will increase in all of the following generations and will thus replace all other alleles initially present in the population. This has as a necessary consequence that there can be at most one allele in the population that shows above average pollen tube growth for all frequencies and in all pistil types.

Result

If heterophasic mating is realized at a diploid, autosomal gene locus with an arbitrary number of alleles, and if all selection prior to mating is excluded (i.e. $2P(T_{ij}) = Q_{ij}$*, and the mating references of the diplophase types are given by equation (9.7)), then there can exist at the most one haplotype (allele) which is preferred above the average (positive) by all diplotypes (diploid genotypes) under all frequency conditions. For separated generations such an allele would become asymptotically fixed in the population.*

For a gene locus with only two alleles, this finding is not very surprising. Only for more than two alleles does an intuitive explanation become difficult, since it is not immediately clear why a globally positive preference for more than one allele should prevent a compensation by other sufficiently negatively preferred alleles. Hence, the above result is not trivial for more than two alleles. However, this situation may change as soon as selection is allowed to occur prior to the matings, in the sense that either equation (9.7) is violated or the types of the diplophase have differential mating success.

NEGATIVE ASSORTATIVE MATING

The definition of homotypic matings is ambiguous in the present model, since the allele of a pollen grain may occur in one or two copies in a pistil type, according to whether the latter is heterozygous or homozygous. Such ambiguity cannot arise with the definition of heterotypic matings if the mating partners are required to share no alleles, i.e. if matings of the type $T_i \times T_{kj}$ with $k \neq i \neq j$ are considered as heterotypic. Clearly, the possibility for heterotypic matings relies on the existence of more than two alleles in the population. Negative assortative mating, which is the topic of the present subsection, can thus be defined for all types of the diplophase by $U_{i\triangleleft kj} \geq 1 + x$ for all $k \neq i \neq j$, where x is any positive constant, and the above conditions for the absence of selection prior to mating ($2P(T_{ij}) = Q_{ij}$) and mating references according to equation (9.7)) are assumed to hold.

Consider the transition equations (9.6) for the allele frequencies, and substitute the mating norms $P_{i\triangleleft jk}$ by $U_{i\triangleleft jk} \cdot R_{i\triangleleft jk}$. It then follows for the allele frequencies in the next generation:

$$\begin{aligned} q_i' &= \tfrac{1}{2} q_i + \tfrac{1}{2} \sum_{j,k} \tfrac{1}{2}(1 + \delta_{jk}) U_{i\triangleleft jk} R_{i\triangleleft jk} Q_{jk} \\ &\geq \tfrac{1}{2} q_i + \tfrac{1}{2} \sum_{\substack{j,k \\ j\neq i\neq k}} \tfrac{1}{2}(1 + \delta_{jk}) U_{i\triangleleft jk} R_{i\triangleleft jk} Q_{jk} \\ &\geq \tfrac{1}{2} q_i + \tfrac{1}{2} \sum_{\substack{j,k \\ j\neq i\neq k}} \tfrac{1}{2}(1 + \delta_{jk})(1 + x)(1 - s) q_i Q_{jk} \\ &= \tfrac{1}{2} q_i + \tfrac{1}{2}(1 + x)(1 - s) q_i (1 + Q_{ii} - 2q_i), \end{aligned}$$

and thus

$$\frac{q_i'}{q_i} \geq \tfrac{1}{2}[1 + (1 + x)(1 - s)(1 + Q_{ii} - 2q_i)].$$

While q_i approaches 0, the quotient q_i'/q_i converges to the limit $\frac{1}{2}[1+(1+x)(1-s)]$. Thus, if this value is greater than 1, i.e. if $x > s/(1-s)$, then the allele A_i will increase in frequency for at least a limited number of generations if it started at low frequency. In other words, *an allele A_i can become established in the population if all of the previously present diplotypes show a positive mating preference for this allele, and if this preference exceeds the reciprocal of* $1 - s$, i.e. for small values of q_i the inequality $U_{i\triangleleft jk} > 1/(1-s)$ holds for all k and j which are not equal to i. High self-pollination proportions s may thus hinder the establishment of an allele even if it is positively preferred by all types of the diplophase.

In a more specific form, this result is well known to be characteristic of so-called “self-sterility systems”, as were found in *Oenothera organensis*, for example, and as were analyzed by Fisher (1958, p.104ff). Fisher applied to his model as additional assumptions the absence of self-pollination ($s = 0$), complete incompatibility of homotypic (non-heterotypic) matings ($U_{i\triangleleft ij} = 0$ for all i), and conditional random mating for heterotypic matings. Consequently, in this case equation (9.7) reduces to $R_{i\triangleleft jk} = q_i$, and conditional random mating with respect to the heterotypic matings implies $U_{i\triangleleft jk} = 1/(1-q_j-q_k)$ for $j \neq i \neq k$ and $j \neq k$ as well as $U_{i\triangleleft jj} = 1/(1-q_j)$ for $i \neq j$. The heterotypic mating preferences of the diplotypes are thus all greater than 1, so that the above conditions for the establishment of an allele are valid.

Two alleles

If only two alleles are involved in the control of differential pollen tube growth, it has to be taken into account that heterotypic mating types, as were defined in the preceding subsection, can now only appear as matings of homozygous diplotypes with haplotypes carrying the alternate allele. Similarly, homotypic matings can unambiguously be defined only for matings between homozygous diplotypes and haplotypes carrying the same allele. Hence, whenever heterozygous diplotypes are involved, neither of these two mating types is realizable. Therefore, the conditions for positive and negative assortative mating involve only homozygous diplotypes and reduce to $U_{i\triangleleft ii} > 1$ and $U_{i\triangleleft ii} < 1$, respectively ($i = 1, 2$). This is equivalent to $U_{j\triangleleft ii} < 1$ and $U_{j\triangleleft ii} > 1$, respectively, for $i \neq j$. Consequently, the total population mates positively assortatively with respect to this gene locus if both $U_{1\triangleleft 11}$ and $U_{2\triangleleft 22}$ are greater than 1. If both these homotypic mating preferences are less than 1, which makes both heterotypic preferences greater than one, negative assortative mating of the whole population is said to be realized.

With this concept in mind and under the assumption of the preceding subsection, the special model introduced in section 9.1 will now be analyzed in more detail. Recall that this model was characterized by the average number N of pollen arriving at a given stigma type and by a (compound) Poisson distribution for the fertilization probabilities. The assumption that all types of the diplophase have identical mating success implies that the parameter N is the same for all (diplo-) genotypes (consult the equation before (9.5)). The set $\mathcal{H}_{ij}$ now consists of only a single type, namely the allele that causes fast pollen tube growth in A_iA_j-pistils.

According to which pollen type causes fast pollen tube growth in which pistil type, different cases can be distinguished. For example, A_1-pollen tubes may grow faster in A_1A_1- and A_1A_2-pistils than A_2-pollen tubes, while the reverse may be true for A_2A_2-pistils. The cases where one pollen type shows superior pollen tube growth in at least one pistil and is not inferior in any of the other pistils need not be considered further here, since the pertinent allele will become globally fixed in the population, as was previously shown. Moreover, all cases which result from each other by merely exchanging the roles played by the alleles A_1 and A_2 will be condensed to a single case. This leaves the seven cases for consideration which are listed in Table 2. In this table, for each of the three stigma types the pollen tube growth of the allele A_1 as compared to the allele A_2 is represented by the symbols '+' for fast (meaning A_1 is faster than A_2), '–' for slow (meaning A_1 is slower than A_2), and '0' for equal speed.

Table 2: *A_1-growth in pistil type*

	A_1A_1	A_1A_2	A_2A_2
(*i*)	+	0	–
(*ii*)	+	–	0
(*iii*)	–	+	0
(*iv*)	+	+	–
(*v*)	–	–	+
(*vi*)	–	0	+
(*vii*)	+	–	+

When viewed in the light of gene action systems, the most interesting cases are those for which the presence of an allele in the pistil impairs growth of pollen tubes if the pollen carries this allele. The opposite would occur if growth is impaired for pollen carrying a different allele. This concept may lead to a conflicting situation in heterozygous pistils, which might either result in equal growth for both pollen types, or, for reasons of a stronger effect of one of the two alleles in the pistil, might result in the same growth conditions as in the pistil homozygous for the allele with the stronger effect. This kind of general interpretation of gene action systems gives less significance to the cases (*ii*), (*iii*) and (*vii*).

The general transition equations for two alleles (accounting for the present assumptions) are obtained from equation (9.6):

$$\begin{aligned}
Q'_{11} =& Q_{11} \cdot P_{1\triangleleft 11} + \tfrac{1}{2} Q_{12} \cdot P_{1\triangleleft 12} \\
Q'_{22} =& Q_{22} \cdot P_{2\triangleleft 22} + \tfrac{1}{2} Q_{12} \cdot P_{2\triangleleft 12} \\
Q'_{12} =& Q_{11} \cdot P_{2\triangleleft 11} + Q_{22} \cdot P_{1\triangleleft 22} + \tfrac{1}{2} Q_{12} \\
q'_1 =& \tfrac{1}{2} [q_1 + Q_{11} P_{1\triangleleft 11} + Q_{22} P_{1\triangleleft 22} + Q_{12} P_{1\triangleleft 12}]
\end{aligned} \tag{9.8}$$

In these equations the conditional mating frequencies $P_{2\triangleleft ij}$ can, of course, be substituted by $1 - P_{1\triangleleft ij}$. The actual form of $P_{1\triangleleft ij}$ for A_1-pollen tubes which grow faster than (+), slower than (–), or at the same speed (0) as A_2-pollen tubes in $A_i A_j$-pistils is obtained from equation (9.3):

$$P_{1\triangleleft ij} = \begin{cases} \dfrac{1 - e^{-N \cdot R_{1\triangleleft ij}}}{1 - e^{-N}} & \text{if } A_1 \text{ is faster in } A_i A_j\text{-pistils than } A_2, \\ \dfrac{e^{-N \cdot R_{2\triangleleft ij}} - e^{-N}}{1 - e^{-N}} & \text{if } A_1 \text{ is slower in } A_i A_j\text{-pistils than } A_2, \\ R_{1\triangleleft ij} & \text{if } A_1 \text{ and } A_2 \text{ are equivalent in } A_i A_j\text{-pistils,} \end{cases}$$

where the mating references result from equation (9.7) as

$$\begin{aligned}
R_{1\triangleleft 11} =& s + (1 - s) \cdot q_1, \\
R_{1\triangleleft 12} =& \tfrac{1}{2} \cdot s + (1 - s) \cdot q_1, \\
R_{1\triangleleft 22} =& (1 - s) \cdot q_1,
\end{aligned}$$

and $R_{2\triangleleft ij} = 1 - R_{1\triangleleft ij}$ holds.

Complete self-pollination (s = 1): In this case $P_{1\triangleleft 11} = P_{2\triangleleft 22} = 1$, $P_{1\triangleleft 22} = P_{2\triangleleft 11} = 0$, and $P_{1\triangleleft 12}$ does not depend on the genotypic frequencies (is constant). One thus obtains with the help of equation (9.8):

$$Q'_{12} = \tfrac{1}{2} Q_{12}, \quad q'_1 = q_1 + \tfrac{1}{2} Q_{12} \cdot (P_{1\triangleleft 12} - \tfrac{1}{2}).$$

This system of difference equations allows for the general explicit solution

$$q_1(t) = q_1 + Q_{12} \cdot (P_{1\triangleleft 12} - \tfrac{1}{2}) \cdot \left[2 \left(1 - \left(\tfrac{1}{2}\right)^{t+1} \right) - 1 \right].$$

Here q_1 and Q_{12} are the respective frequencies in the initial generation, and $q_1(t)$ is the frequency of A_1 in generation t. Hence, one arrives at the following statement:

Result

For complete self-pollination, the heterozygous genotype disappears asymptotically from the population, and the frequency of the allele A_1 *converges to the limit* $q_1 + Q_{12} \cdot (P_{1\triangleleft 12} - \frac{1}{2})$; q_1 *and* Q_{12} *are the respective frequencies in the initial generation.*

According to whether A_1-pollen tubes grow faster than, slower than, or are equivalent to A_2-pollen tubes in A_1A_2-pistils, the conditional mating frequency $P_{1\triangleleft 12}$ is greater than, less than, or equal to 1/2. Hence, for superiority of A_1 in pollen tube growth, its frequency increases as long as heterozygotes exist in the population, although fixation of this allele does not take place as one might have expected intuitively. In an analogous manner, the allele decreases in frequency when inferior in pollen tube growth, and it does not change in frequency if both alleles are equivalent in pollen tube growth. Consequently, under the supposition of complete self-pollination, the cases (*iii*) and (*iv*), the cases (*ii*), (*v*) and (*vii*), and the cases (*i*) and (*vi*) are identical in effect on the dynamics of the genotypic frequencies. It has to be emphasized that the establishment or protection of an allele is not possible in any of these cases, since the equilibrium states approached are indifferent and the frequency of an allele can in these states become arbitrarily small together with its initial frequency.

As compared with the results of the section 6.2 on complete individual self-mating, it is remarkable that there the allele frequencies could not change, while now they can, even though the mating systems appear to be identical. The reason for this difference lies in the fact that the results derived in section 6.2 are based on homophasic mating for the diplophase, while the present model represents a case of heterophasic mating. In contrast with homophasic mating, for heterophasic mating the (male) gametes do not become successful in exactly the proportions with which they are produced by the respective (diplo-) types. Hence, even though segregation distortion is absent in the gametes before fertilization, differential pollen tube growth can produce effects that are equivalent to segregation distortion among the gametes after fertilization. The present model of complete self-pollination provides a particularly clear demonstration of this fact.

Partial self-pollination (s < 1): It would be extremely laborious to analyze the dynamics implied by each of the above-listed seven cases separately and for all parameter combinations. Nevertheless, it is possible to arrive at a satisfactory picture by restricting the analysis to the situation where individual self-pollination is effectively absent ($s = 0$). The results of this analysis will then be compared with numerical examples demonstrating the effect of partial self-pollination ($0 < s < 1$), where the already analyzed extreme case of complete self-pollination will help to complete the picture.

Replacing in the equations (9.8) the conditional mating frequencies $P_{1\triangleleft ij}$ by $U_{1\triangleleft ij} \cdot R_{1\triangleleft ij}$ and taking account of the fact that $R_{1\triangleleft ij} = q_1$ for $s = 0$, one obtains for the change in frequency of allele A_1:

$$\frac{q_1'}{q_1} = \tfrac{1}{2}(1 + Q_{11} \cdot U_{1\triangleleft 11} + Q_{22} \cdot U_{1\triangleleft 22} + Q_{12} \cdot U_{1\triangleleft 12}).$$

As q_1 approaches 0 in this equation, the quotient q_1'/q_1 converges to the limit $\frac{1}{2}(1 + U_{1\triangleleft 22})$, provided that at the same time $U_{1\triangleleft 22}$ converges to a uniquely defined limit. As was shown in connection with the mating preferences in equation (9.4), the latter provision is at least fulfilled for the present model of pollen tube growth.

Consequently, the allele A_1 can become established and is protected, once established, if for small frequency q_1 of A_1 $U_{1\triangleleft 22} > 1$ holds. The allele cannot become established and is not protected if $U_{1\triangleleft 22} < 1$ holds. As was demonstrated subsequent to equation (9.4), a very rare pollen type will be preferred at a rate $U = N/(1 - e^{-N})$ if it is superior in growth and at a rate $U = N/(e^N - 1)$ if it is inferior in growth. For large pollination density N, the pollen allele A_1 will thus become rapidly established if it is superior in growth to A_2 in A_2A_2-pistils, and it will disappear rapidly if it is inferior in growth and already at low frequency. Clearly, this result applies to the problem of establishment of A_1 in all of the above seven cases of pollen tube growth.

The conditions for establishment of the allele A_2 are obtained for the cases (*i*) and (*iv*) – (*vii*) by interchanging the subscripts 1 and 2 in the analysis of the last paragraph. Recalling the definitions of negative assortative ($U_{1\triangleleft 22} > 1$ and $U_{2\triangleleft 11} > 1$) and positive assortative ($U_{1\triangleleft 11} > 1$ and $U_{2\triangleleft 22} > 1$) mating given for two alleles at the beginning of the present subsection, these results can be stated in the following simple manner:

Result

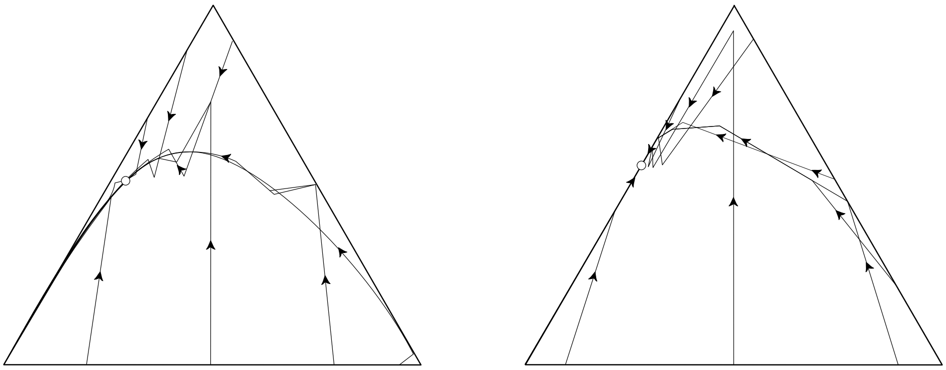
In the absence of self-pollination in the present model, negative assortative mating of the homozygotes protects the biallelic polymorphism, irrespective of the mating behavior of the heterozygote. This protection is very strong for large pollination densities. Positive assortative mating of the homozygotes has the opposite effect in that it implies facultative fixation, irrespective of the behavior of the heterozygote.

Applying this to the above seven cases, one concludes that among these the cases (*v*) and (*vi*) entail protection of the biallelic polymorphism and thus the maintenance of differential pollen tube growth in the population. The cases (*i*) and (*iv*) imply facultative fixation. Furthermore, in the case (*vii*) the allele A_1 is protected and A_2 is not, which includes the possibility of global fixation of A_1, although additional analyses are required to prove this assertion. As was argued earlier, the remaining cases are of lesser biological significance and will therefore not be pursued further.

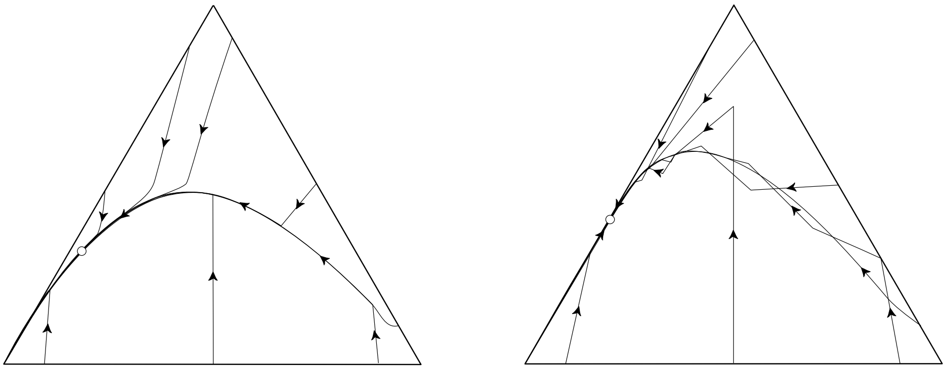
Since a rigorous analytical treatment of the effects of the proportion of self-pollination is very complex, additional possibilities for the dynamics of differential pollen tube growth will be illustrated with the help of numerical examples. Case (*v*) is well suited for this purpose, since it allows the question to be studied as to whether a polymorphism that is protected in the absence of self-pollination may become endangered with increasing proportions s of self-pollination in connection with different pollination densities N. This question is of considerable interest, since self-fertilization is widely accepted to exert destabilizing effects on genetic polymorphisms maintained, for example, by viability selection (see e.g. Kimura and Ohta 1971, p.155 and Appendix A4)

The Figures 7a to 7f confirm this conjecture. In all cases presented, the allele A_2 is more frequent than A_1 in the equilibrium state, which was to be expected from its superiority in growth in two out of three pistil types. For large proportions of self-pollination ($s = 0.9$), even global fixation of the allele A_2 takes place for both pollination densities ($N = 2$ and $N = 5$) considered (see Figures 7c and 7f). However, this tendency appears to weaken with increasing pollination density, as can be suspected from the larger equilibrium frequency of the allele A_2 in Figure 7e as compared with Figure 7b. It is also conspicuous that, for the situation of a protected polymorphism, the frequency of A_1A_1-genotypes is quite low at equilibrium and that this genotype disappears completely for larger polli-

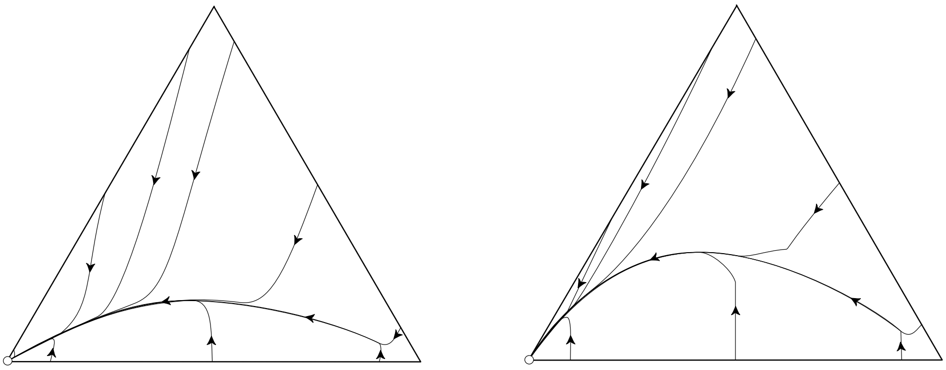
Figure 7



a) $N = 2$, $s = 0$ d) $N = 5$, $s = 0$



b) $N = 2$, $s = 0.5$ e) $N = 5$, $s = 0.5$



c) $N = 2$, $s = 0.9$ f) $N = 5$, $s = 0.9$

Dynamics of the genotypic frequencies in the model for differential pollen tube growth for different pollination densities N *and proportions of self-pollination* s. A_2*-pollen is superior in growth to* A_1*-pollen in* A_1A_1*- and* A_1A_2*-pistils, and* A_1*-pollen is superior in* A_2A_2*-pistils (negative assortative mating).*

nation density (see Figure 7d and 7e). This observation can be explained by the fact that, with increasing pollination density, the allele which is inferior in pollen tube growth in a given pistil type has decreasing chances to participate in the fertilizations, as became evident in Figure 5. Hence, since A_1 pollen is inferior in A_1A_1- and A_1A_2-pistils to A_2-pollen, the genotype A_1A_1 can rarely be produced. At the same time, this promotes the production of heterozygotes, which, in turn, lends plausibility to the observation that high pollination densities aid the maintenance of polymorphisms.

Result

Consider the case where A_2-pollen tubes grow faster in A_1A_1- and A_1A_2-pistils and more slowly in A_2A_2-pistils than A_1-pollen tubes. In this case, the biallelic polymorphism is protected in the absence of self-pollination. The numerical analyses suggest that increasing amounts of self-pollination endanger the polymorphism, but that this tendency is counteracted by high pollination density.

References

Christiansen, F.B. 1977. Population genetics of *Zoarces viviparus* (L.), a review. In: Measuring Selection in Natural Populations. Springer-Verlag, Lecture Notes in Biomathematics 19: 21-47

Darwin, C. 1859. On the Origin of Species. John Murray, London

de Finetti, B. 1926. Considerazioni matematiche sul l'ereditarieta mendeliana. Metron 6: 1-41

Fisher, R.A. 1941. Average excess and average effect of a gene substitution. Ann. Eugen. 11: 53-63

Fisher, R.A. 1958. The Genetical Theory of Natural Selection. Dover Publ., Inc., New York

Gregorius, H.-R., M.D. Ross, E.M. Gillet 1983. Selection in plant populations of effectively infinite size. V. Biallelic models of trioecy. Genetics 103: 529-544

Häcker, M. 1986. Über den Einfluß der zeitlichen Verteilung der Gametenproduktion auf die Fitneß. Göttinger Forstgenetische Berichte 9, 47 pages

Hattemer, H.H., F. Bergmann 1987. Einführung in die Genetik. J.D. Sauerländer's Verlag, Frankfurt am Main.

Karlin, S. 1969. Equilibrium Behavior of Population Genetic Models with Non-random Mating. Gordon and Breach, Sci. Publ.

Kempthorne, O., E. Pollak 1970. Concepts of fitness in Mendelian populations. Genetics 64: 125-145

Kimura M., T. Ohta 1971. Theoretical Aspects of Population Genetics. Princeton: Princeton University Press.

Majerus, M., P. O'Donald, J. Weir 1982. Evidence for preferential mating in *Adalia bipunctata*. Heredity 49(1): 37-49

O'Donald, P. 1980: Genetic models of sexual selection. Cambridge University Press

Ross, M.D., H.-R. Gregorius 1983. Outcrossing and sex function in hermaphrodites: A resource-allocation model. Amer. Nat. 121: 204-222

Ross, M.D., B.S. Weir 1975 Maintenance of male sterility in plant populations. III. Mixed selfing and random mating. Heredity 35: 21-29

Ross, M.D., B.S. Weir 1976. Maintenance of males and females in hermaphrodite populations and the evolution of dioecy. Evolution 30: 425-441

Roux, C.Z. 1977. Fecundity differences between mating pairs for a single autosomal locus, sex differences in viability and nonoverlapping generations. Theor. Population Biol. 12: 1-9

Steiner, W. 1988. Modelle unterschiedlichen Pollenschlauchwachstums und ihre populationsgenetischen Konsequenzen. Masters thesis at the Forstlicher Fachbereich der Universität Göttingen

Subject index

Page numbers appearing in *italics* refer to definitions.