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Chapter 5

THE EVOLUTIONARY DYNAMICS OF MIXED MATING SYSTEMS: ON THE ADAPTIVE VALUE OF SELFING AND BIPARENTAL INBREEDING

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I. ABSTRACT

We present a theoretical approach to the evolution of selfing in natural plant populations that can be applied to general questions addressing the evolution of transmission systems and mate choice. We consider the dependence of the adaptive value of selfing in populations practicing mixed mating systems on the number of offspring produced and the resemblance between parent and offspring. Both factors are themselves influenced by the reproductive mechanism by which the offspring were derived, and by the history of uniparental and biparental inbreeding in the population. We summarize some of the experimental approaches that have been applied to the question, and suggest possible avenues of further empirical and theoretical exploration.

II. INTRODUCTION

The approach of classical quantitative genetics to the analysis of natural and artificial selection rests on two key quantities: heritability and the selection differential [see Falconer (1981), Chapters 10 and 11]. Narrow-sense heritability, which reflects the extent to which offspring resemble their parents, is equal under random mating to the regression of offspring phenotype on midparent phenotype. Natural or artificial selection causes the mean phenotype among reproducing adults to differ from that of the adult population as a whole; the magnitude of this departure is the selection differential. The Galtonian kernel of quantitative genetics proposes that selection leaves the heritability essentially unchanged so that the parent–offspring regression can be used to predict the change in mean offspring phenotype (response to selection) for a given selection differential. The application of this approach to the study of the evolution of breeding systems requires special modification because selection acts on the very mechanism that gives rise to the parent–offspring regression. In his seminal paper on the evolution of self-fertilization, Fisher (1941) showed that restriction of the notion of selection to differences in viability and fertility results in a theory that cannot adequately explain evolutionary changes in reproductive mode. Classical quantitative genetics may be characterized as analyzing the effect of transmission on changes due to selection; in this chapter, we address the natural selection of transmission.

We examine the evolution of self-fertilization, under which transmission of genes is uniparental rather than biparental. This mode of reproduction has at one time or another become established in nearly all hermaphroditic groups, and it has been primarily studied in plants where closely related species (Stebbins, 1957) or even populations within a species (Crosby, 1949; Antonovics, 1968; Jain, 1978) may differ markedly in the frequency of selfing. Discussions have focused on mechanisms under which selfing can be derived from outcrossing, the assumption being that self-fertilization restricts evolutionary potential (Stebbins, 1957) or that selfing represents an irreversible evolutionary trend (Charnov and Bull, 1985).

Bengtsson (1978) portrayed the evolution of breeding systems as a compromise between two conflicting effects of inbreeding: high parent–offspring relatedness and inbreeding depression. Matings between relatives promote the transmission of parental genotypes, but increase the risk of expression of deleterious recessive alleles. The reviews of the theoretical and experimental literature by May (1979) and Bateson (1983) discuss the expected magnitude of inbreeding depression and enumerate

various kinds of costs and benefits which influence the optimal mate choice.

Our analysis of the selective pressures directing the evolution of breeding systems in plant populations addresses the effect of the history of inbreeding in the population on the level of inbreeding depression and on parent–offspring relatedness. While the mean level of inbreeding depression due to completely deleterious recessives held in mutation–selection balance is independent of the breeding system (Haldane, 1937), the relative intensities of inbreeding depression suffered by offspring produced by the various reproductive modes depends upon the extent of prior inbreeding and the magnitude of the difference between the original and introduced breeding systems (Maynard Smith *et al.*, 1955; Morton *et al.*, 1956; Kempthorne, 1957, Chapter 20; Latter and Robertson, 1962). In particular, the introduction of selfing can promote further evolutionary increases in selfing by purging the population of deleterious mutations (Lande and Schemske, 1985). Biparental inbreeding can also exert this effect (Uyenoyama, 1986). Parent–offspring relatedness also depends upon the history of inbreeding (both uniparental and biparental) experienced by the population (Bateson, 1980; Uyenoyama, 1986). Individuals of a given genealogical relationship (e.g., first cousins) will share higher genetic relatedness in populations that experienced higher levels of inbreeding. This dependence of relatedness on historical factors may result in evolutionary shifts in the optimal mate distance (Bateson, 1980).

In this chapter, we consider the evolution of selfing in plant populations within this theoretical framework. We have restricted our discussion of breeding systems to plant populations; much of the work on animals has been reviewed by Bateson (1983). Our objectives are (1) to consider the effects of prior inbreeding on the relatedness between parent and offspring and on the relative success of offspring, and (2) to incorporate some of these effects into an analysis of the evolutionary dynamics of selfing.

III. DETERMINATION OF THE ADAPTIVE VALUE OF SELFING

A. Response of Characters Correlated with Selection

Characters that are positively correlated with fitness increase under natural selection. The covariance between the probability F of survival from birth to reproductive age and a distinct character Z determines the change in the mean value of the second character within a generation:

$$\bar{F}(\bar{Z}^* - \bar{Z}) = \text{Cov}(FZ) \tag{1}$$

where $\bar{Z}$ represents the mean value at birth, $\bar{Z}^*$ the mean at reproductive age, and $\bar{F}$ the mean fitness (Robertson, 1966; Crow and Nagylaki, 1976). In order to extend this analysis over a full generation, we require some description of the relationship between the means for parents $\bar{Z}^*$ and their offspring $\bar{Z}'$. The classical approach to this problem involves calculation of the regression coefficient h^2 of offspring phenotype on parental phenotype to obtain

$$\bar{F}(\bar{Z}' - \bar{Z}) \approx \bar{F}h^2(\bar{Z}^* - \bar{Z}) = h^2 \text{Cov}(FZ) \tag{2}$$

[see Lande and Arnold (1983) for historical and mathematical development]. Implicit in (2) is the assumption that selection does not change the regression coefficient h^2; Kempthorne (1957, p. 329) has shown that this assumption holds strictly only in the absence of dominance. In the absence of selection, the regression of offspring phenotype on midparental phenotype is

$$h^2 = \text{Var}(A_Z)/\text{Var}(Z) \tag{3}$$

where the denominator is the phenotypic variance in the character among parents, and the numerator the additive genetic variance (e.g., Falconer, 1981, Chapter 10). A rearrangement of (2) indicates that the change in the mean character is approximately equal to the product of the additive genetic variance in the character and the regression of the character on fitness:

$$\bar{F}(\bar{Z}' - \bar{Z}) \approx \text{Var}(A_Z)[\text{Cov}(FZ)/\text{Var}(Z)] \tag{4}$$

[Lande (1979); see Lande and Arnold (1983) for the multivariate generalization]. If the character under study is fitness itself, then (4) reduces to Fisher's (1958, Chapter 2) fundamental theorem of natural selection:

$$\bar{F}(\bar{F}' - \bar{F}) \approx \text{Var}(A_F) \tag{5}$$

B. Modification to Accommodate the Evolution of Transmission

Fisher (1941) demonstrated that evolutionary changes in the breeding system do not require variation in conventional measures of fitness (viability or offspring number). The selective component of change in

(1) occurs within generations, with heritability describing the effect of the process of genetic transmission on the response to selection. In contrast, the essence of genetic shifts in breeding systems lies in the selection of the transmission process itself: it is the between-generation component of natural selection that determines the adaptive significance of alternative reproductive modes. Because the transmission process is not a readily observable character, we define fitness as genotypic excess, or the proportional change in genotypic frequency between generations. For example, $T(u'_{11} - u_{11})/u_{11}$ represents the genotypic excess of A_1A_1, where u_{11} is the frequency of that genotype among reproducing adults in the present generation, u'_{11} the frequency in the next generation, and T the average total number of offspring produced among all genotypes. This notion of fitness departs from more conventional measures in that offspring contribute to the fitness of their own genotypes, rather than to the fitness of their parents' genotypes: for example, an offspring having genotype A_1A_1 would be attributed to the genotypic excess of A_1A_1 even if it was produced by a heterozygote. In partially inbred populations, genotypic excess replaces average excess of genes (Fisher, 1941) as the fundamental measure of fitness; both quantities may be regarded as discrete-time analogues of the Malthusian parameter (see Fisher, 1958, Chapter 2; Kimura, 1958; Crow and Nagylaki, 1976). Retrospective measures of fitness (including genotypic excess) possess no predictive power: the most fit genotype is the one that experienced the greatest proportional increase in frequency. However, determination of the conditions under which an evolving character is positively correlated with genotypic excess permits the character measurement itself to serve as a prospective indicator of reproductive success.

We consider a population in which individuals produce three offspring classes: biparental from random outcrosses, biparental from matings with relatives, and uniparental. The numbers of the three kinds of offspring that survive to reproductive age represent three character values associated with the seed parent. Table I records the number of offspring belonging to each of these classes produced by individuals of genotype

Table I. Number of Offspring Produced by Genotype A_iA_j by Means of Random Outcrossing, Mating with Relatives, and Selfing

Offspring class	Number produced
Biparental offspring from random outcrossing	$\sigma_{ij} - \bar{\sigma}$
Biparental offspring from matings with relatives	$\tau_{ij} - \bar{\tau}$
Uniparental offspring	$\pi_{ij} - \bar{\pi}$

A_iA_j. Genotypic value is expressed as a deviation from the mean number of offspring of a particular class, and comprises conventional fitness components including fecundity and viability. For simplicity, we assume that the locus under study does not influence any other component of fitness, including offspring production through pollen. A proportion t of pairings occur between relatives of a specified kind, and $1 - t$ between unrelated individuals. The covariance between genotypic excess and genotypic value associated with random outcrossing is equal to

$$T(\bar{R}' - \bar{R}) = \text{Var}(M_R)[(1 - t)b_{P \to R} + tb_{P \to I}\phi_I + b_{P \to U}\phi_U] \quad (6)$$

with

$$b_{P \to R} = \text{Cov}(M_R O_R^R)/\text{Var}(M_R) \quad (7a)$$
$$b_{P \to I} = \text{Cov}(M_I O_R^I)/\text{Cov}(M_I M_R) \quad (7b)$$
$$b_{P \to U} = \text{Cov}(M_U O_R^U)/\text{Cov}(M_U M_R) \quad (7c)$$
$$\phi_I = \text{Cov}(M_I M_R)/\text{Var}(M_R) \quad (8a)$$
$$\phi_U = \text{Cov}(M_U M_R)/\text{Var}(M_R) \quad (8b)$$

where M denotes variables associated with the seed parent; O^R, O^I, and O^U variables associated with outbred biparental, inbred biparental, and uniparental offspring; and subscripts denote the genotypic value of the corresponding character (see Appendix A).

The covariances in (6) comprise two important determinants of the adaptive value of outcrossing: the resemblance between parent and offspring and the tradeoffs in numbers among the various kinds of offspring. The ratios in (7) describe the resemblance between the seed parent and the offspring; they assume the role of the parent–offspring regressions in (4). For example, the phenotypic relatedness between parent and inbred biparental offspring ($b_{P \to I}$) compares the covariance between one character (inbred biparental offspring production) in the parent and a different character (outbred offspring production) in the offspring to the covariance between these two characters within the seed parent itself. Relatedness increases with the fidelity with which the parental phenotype is transmitted to offspring.

Tradeoffs in offspring number also influence the relative adaptive value of the various reproductive modes considered here. The regression coefficients in (8) express the effect of the production of outbred biparental offspring on the production of other kinds of offspring. The adaptive value of increased investment in one kind of offspring will be limited to the extent to which it is negatively correlated, for either genetic or

developmental reasons, with investment in other components of fitness. Both the sign and the magnitude of the tradeoffs in offspring number depend on the mechanism by which self-fertilization is achieved and the relative timing of selfing and outcrossing (Lloyd, 1979). For example, under "competing self-fertilization" (Lloyd, 1979), an increase in the production of randomly outcrossed offspring results in a decrease in the production of uniparental offspring. If the mechanism by which selfing is achieved entails the production of special morphological features, then the production of uniparental seeds may preclude the production of biparental seeds by a given flower or individual. In such cases, the two forms of biparental reproduction may be positively correlated (ϕ_I positive), and uniparental and biparental reproduction negatively correlated (ϕ_U negative). Alternatively, attraction of pollinators characterized by restricted movements between successive flowers (Schmitt, 1980; Waser and Price, 1983) may result in positive associations between uniparental and biparental inbreeding. In such cases, both ϕ_U and ϕ_I may be negative.

An expression similar to (6), but stated in terms of the change in the mean additive genotypic value associated with outbred biparental offspring production, was studied by Uyenoyama (1986). Consideration of the additive component of variation alone (see Li, 1967; Price, 1970, 1972) provides a direct link to conditions obtained by conventional local stability analysis of recursion systems defined for mating type frequencies, and permits reduction of the parent–offspring comparisons in (7) to more familiar expressions of relatedness.

While a full analysis of the 12-dimensional recursion system (see Appendix A) that led to (6) poses formidable technical difficulties, a heuristic analysis based solely on (6) and using the expressions for relatedness expected under neutrality is clearly feasible. This approach has been tested by the parallel dynamic analysis of the corresponding recursion system in the simpler case studied by Uyenoyama (1986). In the absence of dominance, (7) and (8) reduce to ratios of covariances of additive genotypic values. The additive regression of uniparental offspring on parent is unity (see Uyenoyama, 1984). The additive regression of biparental offspring on parent is $(1 + m)/2$ [see Uyenoyama and Bengtsson (1982), Eq. (11), with $\bar{m}_i = f_i$], where m is the additive correlation between mates. This expression is identical to the equilibrium value of the correlation between parent and offspring obtained by Wright (1921). We set $b_{P \to U}$ equal to 1, $b_{P \to I}$ to $(1 + m)/2$, and (because unrelated individuals are uncorrelated) $b_{P \to R}$ to 1/2 to obtain from (6) an approximate criterion for selfing to be advantageous:

$$(1 - t)/2 + t\phi_I(1 + m)/2 + \phi_U > 0 \qquad (9)$$

C.   Inbreeding Depression and Reproductive Mode of Origin As Determinants of Tradeoffs in Offspring Number

Offspring number depends upon factors associated with differences in reproductive mode (uniparental or biparental) by which the offspring were derived, as well as factors (including inbreeding depression) associated directly with offspring genotype. Lloyd (1980a) distinguished between the "numerical advantages" of uniparental reproduction and the "qualitative superiority" of biparental offspring. We summarize the returns on parental investment in uniparental reproduction relative to biparental reproduction by ϕ. For example, if biparental reproduction entails the production of costly morphological features designed to attract pollinators or provision seeds (see Solbrig, 1976, 1979; Lloyd, 1980b; Schemske, 1978; Waller, 1979; Clay, 1983a), then ϕ will be large, indicating that many uniparental offspring could be produced by reallocating parental investment from biparental reproduction. If, however, differences in mode of dispersal of uniparental and biparental offspring (Schmitt $et\ al.$, 1985) subject the two kinds of offspring to different selective regimes and cause uniparental offspring to suffer higher mortality rates, then ϕ will be small. Considering only the costs associated with parental investment (ϕ) and inbreeding depression (see Appendix B), we obtain an expression for ϕ_U:

$$\phi_U = -\phi\{1 - n\mu/[s + (1 - s)tm]\} \qquad (10)$$

where n is the number of loci contributing to inbreeding depression (multiplicative and additive interactions among loci are indistinguishable to the order of the approximation). The exchange rate between outbred and inbred biparental offspring, derived in a similar way, is

$$\phi_I = 1 - n\mu m/[s + (1 - s)tm] \qquad (11)$$

The difference between the relative costs of inbred biparental offspring and uniparental offspring relative to the former [see (10) and (11)] is approximately

$$(\phi_I - |\phi_U|)/\phi_I = (1 - \phi) + n\mu(1 - m)/[s + (1 - s)tm] \quad (12)$$

Expression (12) indicates that $1 - \phi$ represents an index of the importance of reproductive mode by which offspring were derived as a determinant of variation in number of uniparental and inbred biparental offspring, and $n\mu(1 - m)$ an index of the importance of inbreeding depression. As ϕ approaches unity, the difference in relative success

between these two offspring classes can be attributed primarily to the difference in the level of inbreeding depression. As $n\mu(1 - m)$ approaches zero, the difference between the levels of inbreeding depression suffered by uniparental and inbred biparental offspring becomes negligible.

D. The Effect of Uniparental and Biparental Inbreeding on the Selective Advantage of Selfing

Substitution of (10) and (11) into (9) produces the criterion for the selective advantage of selfing:

$$[s + (1 - s)tm][2\phi - (1 + tm)] > n\mu[2\phi - \bar{t}m(1 + m)] \quad (13)$$

We use (13) to study the evolution of selfing under three systems of regular biparental inbreeding: parent–offspring pairings, matings between full siblings, and matings between individuals having a common seed parent (maternal half-sibs). If inbreeding depression is negligible in comparison to the effect of reproductive mode of origin (uniparental or biparental) in determining offspring number, then (13) reduces to

$$\phi > (1 + tm)/2 \quad (14)$$

(Uyenoyama, 1986). If inbreeding depression represents a significant factor, then (13) determines an upper bound for $n\mu$. In this case, selfing is disadvantageous if (14) is violated; under the condition that (14) holds, we compare the upper bound for $n\mu$ obtained from (13) to the upper bound associated with a population undergoing no biparental inbreeding. In the absence of biparental inbreeding ($t = 0$), (13) reduces to

$$s[1 - 1/(2\phi)] > n\mu \quad (15)$$

Condition (15) reduces to the criterion obtained by Lande and Schemske (1985) in the absence of an effect of reproductive mode of origin on offspring number ($\phi = 1$).

We use these conditions to study the qualitative effect of biparental inbreeding as a factor promoting or discouraging evolutionary increases in the rate of selfing. Our conclusions are based on comparing the conditions permitting an increase in selfing in two populations which are identical in every respect except that biparental inbreeding occurs in the one [$t > 0$ in (13)] but not the other [$t = 0$ in (15)] (see Appendix C).

IV. THREE REGULAR SYSTEMS OF BIPARENTAL INBREEDING

A. Regular Systems of Inbreeding

Path analysis (see Wright, 1921; Li, 1976, Chapter 16) affords a simple method of obtaining the expressions for the correlations among relatives expected in the absence of dominance and selection. The correlation between parent and uniparental offspring is 1, between parent and offspring produced by random outcrossing it is 1/2, and between parent and biparental offspring produced by mating with a relative it is $(1 + m)/2$, where m is the correlation between the relatives involved.

If biparental inbreeding involves parent–offspring matings, then m is equal to the overall parent–offspring correlation r_{PO}, which converges to

$$r_{PO} = (1 + s)/[(1 + s) + (1 - t)(1 - s)] \qquad (16)$$

Substitution of (16) for m in (13) produces the condition for selfing to be selectively advantageous.

For the case of matings between full siblings, three sets of path diagrams were formulated to study the correlations between two uniparental offspring, two biparental offspring, and one of each kind. The overall correlation expected at equilibrium between full sibs is

$$r_{FS} = (1 + s^2)/[(1 + s^2) + (1 - t)(1 - s^2)] \qquad (17)$$

(Uyenoyama, 1986). Expression (17) assumes the same functional form as (16), but with s^2 replacing s, indicating that the effect of selfing on the correlation between mates under parent–offspring mating is greater than that under sib mating.

If pollen flow is restricted in large part to individuals derived from seeds that dispersed to the same location, then biparental inbreeding may involve individuals that had a common seed parent but different pollen parents. Of the five path diagrams required for this case, three depict the relationships between two biparental offspring for which none, one, or all three parents involved were themselves derived from a single seed parent. The equilibrium value for the correlation between maternal half-sibs is

$$r_{HS} = (1 + s)^2/[t(1 + s)^2 + 4(1 - t) + t(1 - t)(1 - s)^2] \qquad (18)$$

B.   The Effect of Prior Inbreeding on the Condition Permitting the Increase of Selfing under Negligible Inbreeding Depression

Condition (14) represents the threshold value for ϕ (the relative success of uniparental offspring) above which selfing is favored. For all three mating systems considered, the threshold value increases with the rates of selfing s and biparental inbreeding t: both uniparental and biparental inbreeding discourage further evolutionary increases in the rate of selfing. The effect of s on (14) suggests that under certain conditions selfing will be favored at low rates, but its evolution will reduce its own selective advantage; such behavior introduces the possibility of evolutionarily stable intermediate levels of selfing (see Lloyd, 1979; Uyenoyama, 1986). The effect of t on (14) indicates that populations that practice biparental inbreeding are less susceptible to the invasion of genes promoting selfing.

The history of both uniparental and biparental inbreeding in the population influences relatedness between parents and their biparental offspring produced from matings with relatives. In the absence of dominance and selection, parent–offspring relatedness assumes the value $(1 + m)/2$, where m is the correlation between mates (see preceding section). Irrespective of the extent of inbreeding in the ancestry of the parents, a single episode of random outcrossing ($m = 0$) would reduce the parent–offspring relatedness to 1/2. Qualitatively different effects of prior inbreeding on parent–offspring relatedness arise under biparental inbreeding ($m \neq 0$). Correlation between mates contributes to correlations between uniting gametes (genes within individuals) and to correlations between relatives (genes between individuals). In the presence of selfing, higher correlations between uniting gametes in turn promote higher correlations between relatives, if one or both were derived by selfing. As a result, both uniparental and biparental inbreeding increase the correlations between potential mates and contribute to high levels of relatedness between parents and their biparental offspring.

C.   The Effect of Biparental Inbreeding on the Adaptive Value of Selfing in the Presence of Significant Inbreeding Depression

Lande and Schemske (1985) demonstrated that the introduction of selfing modifies the conditions permitting further evolutionary increases by reducing the mutational load borne by a population. Selfing promotes homozygosis, which permits the expression and elimination of deleterious recessive genes. Biparental inbreeding also promotes homozygosis, and

may be regarded as a preadaptation for selfing [see Templeton *et al.* (1976) and Templeton (1979) for a critical assessment of this effect on the evolution of parthenogenesis in *Drosophila mercatorum*]. The role of biparental inbreeding in purging deleterious recessives conflicts with its role in increasing parent–offspring relatedness: the former tends to promote selfing, while the latter tends to maintain biparental reproduction. Our comparison of the conditions for the increase of selfing in populations practicing partial biparental inbreeding to those for populations practicing random outcrossing (see Appendix C) indicates that the net effect of biparental inbreeding on the evolution of selfing depends on the extent to which inbreeding depression determines the tradeoffs in offspring number among the three classes.

Biparental inbreeding discourages evolutionary increases in selfing rates for small values of ϕ, the relative success of uniparental offspring expected on the basis of reproductive mode of origin alone. For values of ϕ much less than unity, the importance of inbreeding depression in determining the tradeoffs in offspring number is small [see (12)]. In such cases, the effect of biparental inbreeding in increasing parent–offspring relatedness predominates under all three systems of inbreeding considered here.

Biparental inbreeding promotes evolutionary increases in selfing rates if biparental reproduction is costly (large ϕ). For values of ϕ near or greater than unity, the conditions permitting the increase of selfing are less stringent under biparental inbreeding ($t > 0$). The threshold value of ϕ separating the two zones, which differ with respect to the net effect of biparental inbreeding, lies between $(1 + tm)/2$ and $(1 + m)/2$ for all three mating systems considered (see Appendix C). Under parent–offspring and full-sib matings, this threshold value increases with t. This result implies that biparental inbreeding discourages evolutionary increases in selfing for high rates of biparental inbreeding. However, under matings between maternal half-sibs, the threshold value decreases as t increases for high rates of selfing. This result implies that in populations practicing high rates of selfing, increased levels of biparental inbreeding tend to elevate the importance of inbreeding depression, thereby reinforcing the role of biparental inbreeding as a preadaptation for selfing.

D. A Summary of the Qualitative Effects of Biparental Inbreeding on the Evolution of Selfing

The analytical results described here support the view that biparental inbreeding exerts conflicting pressures on the potential for the evolution of selfing. Biparental inbreeding tends to maintain biparental reproduction

by increasing parent–offspring relatedness, and tends to promote the evolution of selfing by purging deleterious recessives from the population and reducing the viability of inbred biparental offspring. Our preliminary consideration of three regular mating systems (parent–offspring, full-sib, and maternal half-sib) indicates that (1) biparental inbreeding promotes selfing if inbreeding depression represents the major determinant of offspring number [$\phi > (1 + m)/2$], and (2) biparental inbreeding discourages selfing if reproductive mode of origin represents the major determinant of offspring number [$\phi < (1 + tm)/2$]. However, the sensitivity of the effect of increasing t on the threshold value separating these two classes to the kind of inbreeding considered (maternal half-sib differs from full-sib or parent–offspring) suggests that the finer features of the interaction between these opposing trends will depend upon the particular populations involved.

V. DISCUSSION

A. Toward a Predictive Theory of Mating System Dynamics

The determinants of the evolutionary dynamics of mating systems, and selfing in particular, have been largely inferred from geographic and ecological correlates of breeding system variation among closely related taxa or populations (Stebbins, 1957; Levin, 1972; Antonovics, 1968; Lloyd, 1965; Wyatt, 1984b, 1986). Indeed, the study of breeding system evolution in plants is remarkable for a dearth of empirical data that can be used in any predictive manner to study the actual dynamics of breeding system evolution, in spite of the abundance of studies in breeding system variation and of speculations as to the evolutionary origins and consequences of such variation. Much of this may in large measure be due to the lack of a theoretical foundation (such as has been present for conventional quantitative traits) on which to base predictive empirical studies.

Our treatment of evolutionary changes in the rates of production of uniparental and biparental offspring serves as a theoretical framework from which an empirical understanding of the adaptive value of selfing may be developed. This approach (6) indicates that the relative adaptive value of alternative breeding systems depends upon (1) the genetic variance in reproductive mode, (2) the mating system in biparental crosses and the relatedness between maternal parents and the different kinds of offspring they produce, and (3) the relative costs of uniparental and biparental offspring, which reflect offspring viability as well as demands on maternal resources. In this section, we describe direct empirical estimates

of certain of these determinants of reproductive success, discuss some of their implications, and suggest possible avenues of further empirical and theoretical development.

B. Genetic Variation in Reproductive Mode

The magnitude of genetic variation in reproductive mode [$\text{Var}(M_R)$ in (6)] determines the rate, but not the direction, of evolutionary change. Genetic variation in selfing rates has mostly been studied in species that show variation in morphological correlates of selfing, such as flower size (Wyatt, 1984a), floret type (Marshall and Abbott, 1984), anther orientation (Lloyd, 1965), and cleistogamy (Schemske, 1984). Clay (1982a) estimated broad-sense heritabilities of the percentage of cleistogamous (closed, obligately selfed) flowers produced in *Danthonia spicata* as 52.6% for plants grown in the field and 71.6% for plants grown in the greenhouse. These figures suggest that the genetic component of variance in morphologies correlated with reproductive mode is substantial.

Genetic variation in selfing rate has been demonstrated by measuring seed set in bagged inflorescences (Antonovics, 1968), but this may not reflect levels of selfing in open-pollinated systems. For example, Lefebvre (1976) showed that while populations of *Armeria maritima* selfed at substantial rates when bagged, selfing in a natural, open-pollinated population was not detectable by monitoring of a genetic marker. The estimation of environmental and genetic contributions to variation in selfing rate requires pedigreed populations in which genotypes are randomized with respect to environmental variation. This is of course directly equivalent to the methodology of estimation for a quantitative trait, but to our knowledge such estimation has never been carried out for a breeding system trait.

C. The Resemblance between Parents and Their Offspring

Parent–offspring relatedness reflects the way in which genetic variation is transmitted between generations. The distribution of genotypes among offspring and, consequently, parent–offspring relatedness depend upon the reproductive mode by which the offspring were derived. Our measure of relatedness (7) assumes the role of heritability in conventional treatments of the response to selection. In the absence of dominance,

relatedness between parent and uniparental offspring $b_{P \to U}$ is 1, between parent and randomly outcrossed biparental offspring $b_{P \to R}$ is 1/2, and between parent and inbred biparental offspring $b_{P \to I}$ is $(1 + m)/2$ [see Uyenoyama (1986) and (9)]. Individuals of *Danthonia spicata* bear both chasmogamous (open, potentially outcrossed) flowers and cleistogamous (closed, obligately selfed) flowers. Clay (1982a) obtained an approximate value for the fixation index F in a natural population of this species by comparing the within-family genetic variance to the between-family genetic variance. This estimate exceeded the value expected based on the frequency of chasmogamous (CH) and cleistogamous (CL) flowers under the assumption that all CH flowers receive pollen from unrelated individuals, and was interpreted as an indication that CH flowers practice high rates of selfing.

It is likely that most plant populations have substantial biparental inbreeding. Plants are sessile, with relatively short pollen and seed dispersal distances (Bradshaw, 1972; Levin and Kerster, 1974), and there is evidence of population substructuring from electrophoretic data (Schaal, 1975). The observation of inbreeding depression in close-neighbor crosses (Price and Waser, 1979) also indicates relatedness between neighbors. Genetic analyses of mating structure have been done in social insects (Ward, 1983), but studies of this kind are just beginning in plants.

A direct analysis of relatedness between mates requires a genetic analysis of parents and their offspring and an independent estimate of the rate of selfing. Using electrophoretic data obtained from natural populations of *Impatiens capensis*, Waller and Knight (1986) estimated F values for parents and offspring derived from CH and CL flowers. Their analysis indicates that the average correlation m between parents of CH offspring lies between 0.4 and 0.5. Because geitonogamy (selfing due to cross-pollination among flowers produced by the same plant) occurs at a low rate [0.086 (Waller, 1980)], this estimate suggests that outcrossing involves mating with close relatives.

D. Empirical Estimates of Tradeoffs in Offspring Number

Tradeoffs in offspring number (8) reflect constraints on allocation of resources available for reproduction as well as offspring viability. For example, associations between the numbers of uniparental and biparental offspring produced may be influenced by the energetics of producing one set of morphological features at the expense of another set (Schemske, 1978; Waller, 1979), pollinator limitation of biparental seed set (Bierzychudek, 1981), inbreeding depression (Schoen, 1982, 1983; Waller,

1984; Clay and Antonovics, 1985), or reproductive success through pollen (Schoen and Clegg, 1985). Evidence of inbreeding depression in outbred cultivated crops and animals is legion, and is also found in experimental and captive populations (Senner, 1980). Such studies indicate that inbreeding depression is important in nature. However, only rarely have these forces been measured in natural populations with mixed mating systems. The measurement of "Darwinian" fitness of selfed, inbred, and outbred progeny requires not only individual survival and fecundity, but also consideration of their relative dispersal distances and dormancy [which may be quite different among floral types (Clay, 1983b; Venable and Lawlor, 1980; Schmitt et al., 1985)] as well as the effect of progeny variance (Waller, 1985).

In *Impatiens* (Schemske, 1978; Waller, 1979) and *Danthonia* (Clay, 1983a), two groups which produce both CH flowers and CL flowers, biparental reproduction entails greater parental expenditure to support the production of floral tissues, nectar, and pollen. Further, seeds derived from CH flowers require longer development times and survive with lower probability than seeds from CL flowers in *Impatiens capensis* and *I. pallida* (Schemske, 1978; Waller, 1979). Mature CH seeds require about 2.5–3 (Schemske, 1978) or 1.5–2 (Waller, 1979) times as much maternal expenditure as CL seeds, based on a consideration of the energy required to produce the necessary morphology as well as the seeds themselves.

Our notion of relative cost of biparental offspring (8) is summarized by the regression of the number of uniparental offspring on the number of biparental offspring. Because the production of both kinds of seeds is correlated with dry weight (Waller, 1979), the numbers of mature CH and CL seeds tend to be positively correlated in *I. capensis* (Waller, 1979) and *Danthonia spicata* (Clay, 1982b). By viewing the number of CL seeds as the dependent variable determined by the number of CH seeds and dry weight, we obtain an estimate of the relative cost of biparental offspring as defined in (8) by calculating the partial regression coefficient of CL seed on CH seed. Waller (1979, Table 1) reported dry weights, together with numbers of buds and seeds derived from CH and CL flowers, for six plants. A multiple regression analysis based on these data explained 93% of the variance in the number of CL seeds in terms of variation in the number of CH seeds and dry weight. Our estimate of the regression of CL seed on CH seed (-3.26 ± 0.68) indicates that about three CL seeds must be forgone to support the production of a single CH seed. This estimate differs significantly ($0.01 < p < 0.025$, one-tailed t-test) from the value (-1) expected were CH and CL seeds equally costly, but does not differ significantly from Waller's estimate of relative cost based on a consideration of energetics in the same population.

E. Long-Term and Short-Term Effects of Selfing on Progeny Variance

Much of the theoretical costs attributed to selfing have focused on inbreeding depression, particularly as a result of deleterious recessives. Inbreeding depression reflects the effects of selfing on offspring mean, but ignores the consequences of selfing on offspring variance. While selfing may have the overall long-term effect of reducing genetic variance, its effects on progeny variance are complex (Robertson, 1952): inbreeding (both uniparental and biparental) has the initial effect of increasing within-family variance in an outcrossing population, even though its long-term effect is the opposite. Selfing may therefore become established as a mechanism to generate within-family variance, and even persist in situations where such selfing is no longer advantageous. Moreover, the prediction that selfing should predominate after deleterious genes are purged by an episode of selfing ignores any counterbalancing forces favoring genetic variance among the progeny or among the grandchildren of outcrossed progeny. The immediate effects of inbreeding in an outbred population are therefore to decrease progeny mean fitness and to increase progeny variance in fitness; this latter factor may correlate positively with "net fitness" (Lacey *et al.*, 1983). The effects of inbreeding in a long-term inbred population are almost the reverse: inbreeding may have little effect on mean progeny fitness relative to outcrossing, whereas it will decrease variance in traits among the progeny. Variance in fitness is likely to be a more important component than mean fitness (1) in environments that are variable in space and time, (2) in environments that are biotically complex such that frequency-dependent effects are legion, and (3) under conditions of high density such that the effects of inbreeding on mean fitness are accentuated by intraspecific competition. The idea that progeny variance is an important fitness component has rarely been tested either in experimental or field populations. A comparison of clonal and variable progeny arrays (Ellstrand and Antonovics, 1985) showed large fitness differences.

F. The Effect of Selfing on Male Success

The theoretical developments in this chapter have assumed that there is no effect of selfing on male success. For example, in *Gilia achilleifolia* the degree of protandry determines in large part the selfing rate, with little reduction in the ability to pollinate other plants (Schoen, 1982, 1983). However, a reduction in male fecundity (pollen discounting) will accompany selfing resulting from partial or total cleistogamy, or increased geitonogamy due to changes in inflorescence architecture, plant size, or

pollinator attractiveness. This will have direct effects on individual fitness of selfed individuals, and influence whether overall pollen limitation in the population becomes important in determining seed set.

G.   Implications of Biparental Inbreeding for the Adaptive Value of Selfing

Our analysis indicates that biparental inbreeding may have conflicting effects on the prospects for evolutionary increases in the rate of selfing, depending upon the importance of inbreeding depression. Lande and Schemske (1985) showed that because the intensity of inbreeding depression suffered by uniparental offspring is directly proportional to the fixation index among uniparentals relative to that of the population as a whole, selfing promotes further increases in selfing. Biparental inbreeding also promotes selfing by purging the population of deleterious recessive mutations and by permitting the level of inbreeding among biparental offspring to approach that among uniparental offspring [see Appendix B and Lloyd (1979) and Uyenoyama (1986)].

Opposing this effect on inbreeding depression is the increase in parent–offspring relatedness under biparental inbreeding. While a single random outcross reduces the parent–offspring regression to 1/2, both uniparental and biparental inbreeding increase relatedness between parents and their offspring derived from crosses to relatives (see preceding section). Higher relatedness between parent and biparental offspring serves to maintain biparental reproduction by reducing the cost of meiosis relative to selfing. The net result of these antagonistic effects of biparental inbreeding depends upon the relative importance of inbreeding depression and parental expenditure as determinants of the relative costs of the various kinds of offspring [see (12) and preceding section]. If the expression of deleterious mutations represents the primary determinant of offspring number, then biparental inbreeding may serve as a preadaptation for selfing. If demands upon parental expenditure predominate, then biparental inbreeding tends to preserve biparental reproduction by reducing the genetic cost of outcrossing [or "cost of meiosis"; see Williams (1980)].

H.   Consequences of Environmentally Imposed Shifts in the Breeding System

Variation in the frequency of uniparental and biparental inbreeding may result from environmental as well as genetic factors. In particular, environmentally imposed changes in the breeding system may have a

substantial effect on the likelihood that genes determining selfing will spread in the population. For example, the "reproductive assurance" hypothesis states that if cross-fertilization is prevented by some environmental circumstance, then immediate fecundity advantages accrue to those genotypes that can produce progeny by selfing. This hypothesis has been used to explain the establishment of selfing in normally outbred populations as a result of adverse environmental conditions disfavoring cross-pollination (Stebbins, 1957), flowering prior to pollinator emergence (Lloyd, 1965), lower density and consequently reduced pollinator service (Baker, 1955), and competition for pollinators (Wyatt, 1986). Cases in which selfing serves as an isolating mechanism preventing the influx of disfavored alien genes from neighboring populations (Antonovics, 1968) may also be subsumed in this category. Environmental forces determining the establishment of selfing may act in a much more complex manner than by means of a simple "reproductive assurance" advantage. The dynamics of the process whereby selfing genes are established in populations may be complex and at times set in motion by past events that may be difficult to infer from present-day processes.

Environmental effects may have a number of consequences for the breeding system.

1. Change in female fecundity. In wholly or largely self-incompatible populations, reduction in pollinator service or decreased density affecting pollen transfer will result in reduced seed set by outcrossing and favor selfing. This effect forms the basis of the "reproductive assurance" hypothesis for the origin of selfing.

2. Change in male fecundity. Decreased pollinator service, precocious flowering, or decreased density may result in reduced male fecundity. Female fecundity may or may not be affected, depending on whether seed set is primarily resource- or pollinator-limited. In the former case, there may be large decreases in pollinator service with little or no effect on seed set.

3. Change in level of uniparental inbreeding. Systems in which the level of facultative selfing depends on environmental factors are well known in plants.

4. Change in level of biparental inbreeding. Even in self-incompatible species, changes in pollinator type and pollinator behavior may have direct effects on probability of mating with relatives, particularly in a spatially substructured population. Changes in the overall level of inbreeding may also result from the founding of populations by a few individuals, or strong selection leading to the success of a group of related individuals sharing a particular trait.

Table II summarizes the various types of environmentally induced breeding systems and their consequences for male and female function, for level of selfing, and for level of genetic correlation among parents.

These environmentally induced changes may be long-term, lasting over many generations, or they may be transient, occurring perhaps only as a pulse effect in one reproductive season. It is easy to envisage that new transmission properties established as a result of transient environmental events may continue to be the dominant force in the system, even if environmental conditions return to their original state. Such transient effects further increase the difficulty of interpreting field data bearing on the evolution of selfing. While the simplicity of "reproductive assurance" explanations are often appealing, they may fail partly or wholly to reflect the evolutionary mechanisms involved.

I. Summary

The complexity of the dynamics of breeding system evolution and the likelihood that such dynamics are influenced by transient events argue for caution in the evolutionary interpretation of existing patterns of breeding system variation. Theoretical treatments also reveal a need for more empirical data on quite fundamental phenomena such as levels of environmental and genetic contributions to variation in mating systems, levels of biparental inbreeding, and fitness estimates based on realistic simulations of dispersed progeny arrays.

- Although many of the ingredients for examining the evolutionary dynamics of mating systems have been studied individually, their integration and application in even one system is at present lacking. Clearly a sound assessment of hypotheses relating to the evolution of mating systems requires a much larger body of empirical data than is available at present. Certainly some simplistic dogmas should be set aside, since they have no empirical basis. We really do not know that selfing is always a derived condition, that selfing is favored in a uniform environment, that selfing becomes established because pollinators are lost, or that selfing represents an "all-or-none" genetic change where mixed mating systems are rare. Such interpretations can be imposed *ex post facto* on existing correlations, but will remain unsubstantiated speculations until empirical tests are developed.

Table II. Summary of Probable Effects of Different Kinds of Environmentally Imposed Changes in the Breeding System on Male Function, Female Function, Uniparental Reproduction (Selfing), and Biparental Inbreeding on Facultative (F) and Obligate (O) Outcrossers[a]

Environmentally imposed change	Effect on facultative (F) or obligate (O) outcrosser			
	Male fecundity	Female fecundity	Selfing vs. outcrossing	Biparental inbreeding
A. Loss of pollinators	Decreased	Unchanged (F) or decreased (O)	Increased (F) or unchanged (O)	Unchanged
B. Bottleneck	Unchanged	Unchanged	Unchanged	Increased in $t + 1$
C. Change in population structure				
1. Lower density	Decreased	Unchanged (F) or decreased (O)	Increased (F) or unchanged (O)	Decreased
2. Shorter pollen dispersal	Unchanged or decreased (if pollen competition)	Unchanged	Unchanged	Increased
3. Shorter seed dispersal	Unchanged	Unchanged or decreased (if seedling competition)	Unchanged	Increased in $t + 1$
D. Strong directional selection	Unchanged	Unchanged	Increased (F) or unchanged (O)	Increased

[a]The effects on biparental inbreeding may be immediate (i.e., result in an increased correlation among mates in the generation in which the effects are imposed) or they may occur in subsequent generation ($t + 1$). Selfing may also result in an increased level of biparental inbreeding in subsequent generations, but this is not explicitly considered. It is assumed that in (A) the amount but not distance of pollen transfer is reduced, in (B) that there is a change in population size, but not density, in (C1) that pollen dispersal distance is unchanged, in (C2) that the amount of pollen transferred is unchanged.

VI.   APPENDIX A

Three genotypes and six mating types can be formed from two alleles at the locus controlling reproductive mode. Because the fertility of a given mating may depend upon whether the individuals involved are related, we distinguish random pairings from those formed between relatives. The frequencies of the six mating types involving relatives (denoted $\bar{b}_i$, $i = 1$–6) sum to t, and the six random pairings (denoted b_i^*, $i = 1$–6) sum to $1 - t$. For any given mating pair the overall frequency is equal to the sum of the frequencies of the mating pair for related and unrelated individuals ($\bar{b}_i + b_i^* = b_i$). In general, the mating type frequencies will differ depending on the relationship between mates ($\bar{b}_i \neq b_i^*$), but the genotypic frequencies among related and unrelated pairs will be identical in the absence of sexual selection. This last assumption implies that individuals enter into pairings with relatives or nonrelatives with probabilities which are independent of their genotypes at the locus under study.

We define fitness F_{ij} of genotype A_iA_j as the sum of three random variables which represent the numbers of offspring of that genotype produced by the three modes of reproduction. The b_i^* sum to $1 - t$, the frequency of mating pairs formed between unrelated individuals, and the $\bar{b}_i$ sum to t, the frequency of mating pairs formed between relatives. The average number of biparental offspring having genotype A_iA_j produced per pair of nonrelatives is R_{ij}, with I_{ij} the average number for inbred matings. The average number of uniparental offspring produced per brood is U_{ij}. These three components sum to F_{ij}:

$$F_{ij} = (1 - t)R_{ij} + tI_{ij} + U_{ij} \qquad (A1)$$

The maternal genotypic values shown in Table I determine R_{ij}, I_{ij}, and U_{ij}. Multiplying both sides of (A1) by the genotypic value of A_iA_j associated with random outcrossing and averaging over all genotypes produces

$$\text{Cov}(FO_R) = T(\bar{R}' - \bar{R}) \qquad (A2a)$$
$$= (1 - t)\,\text{Cov}(M_RO_R^R) + t\,\text{Cov}(M_IO_R^I) \qquad (A2b)$$
$$+ \text{Cov}(M_UO_R^U)$$

where $\bar{R}' - \bar{R}$ represents the change in the mean number of outbred biparental offspring; M_R, M_I, and M_U are the genotypic values of the seed

parent associated with the production of outbred biparental, inbred biparental, and uniparental offspring, respectively; and O_R^R, O_R^I, and O_R^U are the genotypic values associated with outbred biparental offspring production of offspring that were themselves derived by outbred biparental, inbred biparental, and uniparental reproduction.

Equation (A2a) follows from the definition of fitness as the change in genotypic frequency between generations:

$$
\begin{aligned}
Cov(FO_R) &= \sum_i \sum_{j \geq i} u_{ij} R_{ij} T(u'_{ij} - u_{ij})/u_{ij} \\
&= T \sum_i \sum_{j \geq i} (u'_{ij} - u_{ij}) R_{ij} \\
&= T(\bar{R}' - \bar{R})
\end{aligned}
\tag{A3}
$$

Equation (6) represents a rearrangement of (A2) to produce an expression that distinguishes between heritability (7) and relative costs (8).

VII. APPENDIX B

Following Lande and Schemske (1985), we obtain rough approximations of the effect of inbreeding depression on the expected tradeoffs among offspring classes by comparing the mean viability among inbred (both uniparental and biparental) offspring to that among randomly outcrossed offspring. The rate at which completely recessive deleterious mutations are purged depends on their frequency q, the rate at which they are expressed, which depends upon the level of homozygosis F [Wright's fixation index; see Wright (1969, Chapter 7)], and the relative viability of affected carriers $1 - \omega$. At equilibrium, the mutation rate μ is approximately

$$
\mu = qF(1 - \omega)
\tag{B1}
$$

(Haldane, 1937; Crow, 1970).

Each of the three offspring classes considered here is characterized by a distinct fixation index, which implies that mutational load differs among classes. Randomly outcrossed offspring have a fixation index of zero, with F_U and F_I the fixation indices among uniparental and inbred biparental offspring, respectively. Assigning the average viability of randomly outcrossed offspring as unity, one obtains the average fitness of uniparental offspring [using (B1)] as

$$1 - \mu F_U/F \tag{B2a}$$

(see Lande and Schemske, 1985), and that of inbred biparental offspring as

$$1 - \mu F_I/F \tag{B2b}$$

(see Uyenoyama, 1986). The three fixation indices are related by

$$F_U = (1 + F)/2$$
$$F_I = mF_U \tag{B3}$$
$$F = sF_U + (1 - s)tF_I$$

where s is the frequency of selfing in the population and m is the correlation between mates in inbred biparental matings. Simultaneous solution of (B2a) and (B3) produces (10), an expression for the cost of selfing relative to random outcrossing based on a consideration of parental investment and inbreeding depression.

VIII. APPENDIX C

If, for a given system of biparental inbreeding, the upper bound obtained from (13) exceeds that from (15), then we conclude that biparental inbreeding promotes selfing because (15) implies (13), and yet cases can be constructed in which (13) holds but (15) is violated. The first point implies that if selfing is favored in randomly outcrossing populations, it must also be favored in populations undergoing biparental inbreeding; the second point implies that under certain conditions genes promoting selfing will increase in populations undergoing biparental inbreeding even though they fail to increase in randomly outcrossing populations. If the upper bound from (13) is less than that from (15), then we conclude that biparental inbreeding discourages selfing.

In populations experiencing significant inbreeding depression, biparental inbreeding promotes selfing under high costs of biparental reproduction (large ϕ), but not under low costs (small ϕ). For the mating systems under study, the threshold value of ϕ demarcating the two zones lies between $(1 + tm)/2$ and $(1 + m)/2$, and is defined implicitly as a function of the rate of biparental inbreeding t by the larger root of

$$(2\phi - 1)[2\phi(1 - s) + s(1 + m)] - 2\phi[s + (1 - s)tm] = 0 \quad (C1)$$

Equation (C1), the condition under which the randomly outcrossing population and the inbreeding population are equally susceptible to the invasion of selfing, is obtained by setting the bounds determined by (13) and (15) equal to one another. Implicit differentiation of ϕ^* with respect to t (see Courant, 1936, Chapter III) indicates that ϕ^* increases with t under parent–offspring and full-sib matings, but decreases for s approaching unity under maternal half-sib matings. These results support our conclusion that the effect of biparental inbreeding on evolutionary increases in selfing depends upon the kind of inbreeding under consideration.

IX. ACKNOWLEDGMENTS

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