

## Chapter 8

# Life History Variation in Dioecious Plant Populations: A Case Study of *Chamaelirium luteum*

THOMAS R. MEAGHER and JANIS J. ANTONOVICS\*

### Introduction

Perhaps the most commonly acknowledged genetic polymorphism in animal populations is that of sexual dimorphism. Studies on this phenomenon in animal species have shown that sexual dimorphism influences almost every aspect of their ecology and evolution (e.g., Bartholemew 1970, Feduccia and Slaughter 1974, Jackson 1970, Morse 1968). Although perhaps not so conspicuous for plant species, sexual dimorphism can have far-reaching effects on their biology as well. Studies on sexual dimorphism in plants in the past have been largely limited to floral characteristics (Lloyd and Webb 1977), but over the past few years there has been a growing interest in manifestations of sexual dimorphism in plant life histories (Grant and Mitton 1979, Hancock and Bringhurst 1980, Lloyd and Webb 1977, Onyekwelu and Harper 1979, Wallace and Rundel 1979, Willson 1979). In order to elucidate the role of life histories in the evolution of dioecious plant species, it is necessary to study how sexual dimorphism influences the life histories of males and females and, in turn, how sexual dimorphism in life history traits, such as mortality and fecundity, influences the relative roles of males and females in the population as a whole.

The influences of male and female differences on overall life history for plants and animals share some common principles. Perhaps the most obvious point is that the female contribution to population dynamics is more conspicuous in the observable generation of seed or offspring, and so more conducive to measurement. However, by exclusively emphasizing female contributions, most past studies have only investigated approximately half (depending on the sex ratio) of the genotypes in the population. It remains possible that the other half of the genotypes, i.e., the males, may show very different traits that influence the observed characteristics of the overall populations (Keyfitz 1977).

Another major drawback of observing only female life history traits is that this approach is based on the assumption that the dynamics of the female subpopulation is independent of the male subpopulation, which is clearly not the case for any sexually

\*Department of Botany, Duke University, Durham, North Carolina 27706 U.S.A.

reproducing species. For example, female reproductive output is going to depend on the availability of and abundance of the male component of the population. A realistic population projection has to take into account life history traits of both sexes and their interaction. This "problem of the sexes" has been almost the exclusive domain of theoreticians and human demographers (e.g., Das Gupta 1972, 1976, Goodman 1953, 1967, Mitra 1976) and has received little if any attention in the context of natural populations in the zoological and botanical literature.

In most plant species, the impacts of male sexuality and female sexuality on life history are confounded because they take place within the same individuals (cf. Lloyd 1976, 1979b). Dioecious plant species are therefore ideally suited to analysis of the relative impacts of maleness and femaleness on life history because populations of such species consist of separate male and female individuals. Male reproductive contribution can be assayed conveniently by observing whether or not an individual male plant flowers. Thereby it can be determined, for a particular flowering season, which males are most likely to have contributed gametes to the seed crop for that year. If pollen dispersal profiles were known, it would even be possible to assess the relative genetic contribution of particular males on the basis of their proximity to particular females. Even in the absence of such detailed distributional information, the average contribution per flowering male can still readily be assessed. For example, if only a fraction of the males present were in flower in a given season, or if the population sex ratio were shifted toward an excess of females, then the average contribution per male would be increased.

This chapter addresses the contrast between male and female life histories of the dioecious long-lived forest floor herb, *Chamaelirium luteum*. The overall morphology and natural history of *C. luteum* (described in Meagher 1980) make it very amenable to life history studies. Plants occur as basal rosettes with no vegetative spread; therefore individuals readily can be identified. The species has a discrete breeding season, flowering in mid-May; only 10-20% of the individuals in a population flower in a given year. Production of new rosette leaves only occurs once a year in the spring. Moreover, this species shows no sex changes (Meagher 1980), even though the sexes are spatially segregated (Meagher 1980) and there is a strongly male-biased sex ratio (Meagher 1981).

Life history studies on natural populations were conducted in four North Carolina sites designated as Natural Area, Seawell, Silver Hill, and Botanical Garden and described in Meagher (1980). In addition, an analysis was conducted of genetic variation in life history and differences between flowering males and females raised under controlled conditions in the Duke University Phytotron.

Overall, this chapter addresses the following specific questions. What are the genetic differences underlying sexual dimorphism in life history traits in *Chamaelirium luteum*? How are such genetic differences between males and females manifested in the real world under natural conditions? Is there an ecological component to observed sex-specific life history variation in natural populations of *C. luteum*? How are the consequences of the reproductive efforts of male and female individuals reflected in their immediate life history characteristics? What are the effects of observed differences between males and females on long-term population projections? Finally, what are the constraints on life history evolution imposed by male and female sexuality?

### Resource Allocation Under Standard Conditions

In order to assess the genetic component of life history variation, a series of plants was raised from seed in the Duke University Phytotron. These plants, representing 30 seeds for each of 30 half-sibships, were taken through a number of flower induction cycles consisting of artificial "summers" and "winters" (see Meagher 1981, for description of the growth conditions) until they flowered. As plants came into flower their sex was recorded and they were either harvested or retained for future analyses.

The sex ratio both within and among half-sibships was found to be 1:1 as of the time when most of the plants had flowered (Table 8-1; see also Meagher 1981), indicating that the sex ratio bias observed among adult plants in natural populations results from secondary ecological and life history effects and not from a bias in the sex ratio among seedlings. However, there were sex-specific patterns observed in the number of induction cycles until plants flowered for the first time, i.e., age at first reproduction (Table 8-2). Males clearly tended to flower earlier in their lives than did females. A similar difference in age at first reproduction has been reported for only one other dioecious plant species (Godley 1976); differences in age at first reproduction of males and females have been noted for a variety of animal species (e.g., Nagel 1979, Ainley and DeMaster 1980). There was also significant heterogeneity (log-likelihood ratio test; Bishop et al. 1975) among half-sibships in age at first reproduction (Natural Area  $G^2 = 82.3$ , 45 d.f.,  $p < 0.005$ ; Silver Hill  $G^2 = 76.3$ , 45 d.f.,  $p < 0.005$ ; Botanical Garden  $G^2 = 135.0$ , 45 d.f.,  $p < 0.005$ ), suggesting that there is genetic variation for age of first reproduction beyond the effect of sex. There have been very few studies that have investigated genetic variation for age at first reproduction, and these few (e.g., Lewontin 1965), in contrast to our findings for *C. luteum*, have indicated very little genetic variation for this trait.

A subsample of 52 male and 52 female plants for 19 half-sibships flowering for the first time following the fourth induction period was harvested and analyzed for dry weight of rosette leaves, rhizome, roots, and reproductive structures. The data were subjected to a crossed partial hierarchical analysis of variance (Brownlee 1960) of sex by half-sibship nested within site of origin. In this analysis, variation among half-sibships within populations and among sexes are both measures of genetic variation, the former a measure of variation from genetic effects other than sex and the latter a measure of genetic variation attributable to sexual dimorphism.

Table 8-1. Pooled half-sibship sex ratios among plants that have flowered in the Duke University Phytotron

Site	Males/females <sup>a</sup>
Natural Area	1.01 (253)
Silver Hill	1.30 (209)
Botanical Garden	1.06 (237)

<sup>a</sup> Sample size in parentheses. None of these sex ratios showed a significant departure from 1:1 when tested using log-likelihood ratio tests (Bishop et al. 1975).

Table 8-2. Average "age" at first reproduction for plants raised under standard conditions.

Site	Males	Females	G <sup>2</sup> (5 d.f.) <sup>a</sup>
Natural Area	3.5	4.1	27.2 <sup>b</sup>
Silver Hill	4.3	4.6	21.6 <sup>b</sup>
Botanical Garden	3.0	3.7	25.2 <sup>b</sup>

<sup>a</sup> Males and females are compared using a log-likelihood ratio (G<sup>2</sup>; Bishop et al. 1975).

<sup>b</sup> p < 0.005.

Mean values for these characteristics (Table 8-3) showed significant differences between males and females for dry weight of roots and reproductive structures (Table 8-4). Dry weight measurements of roots and reproductive structures also show significant variation among half-sibs, indicating that there exists genetic variation for these characters in addition to the overall sex differences. Rosette leaf number was found to be highly correlated with total dry weight ( $r = 0.83$  for males;  $r = 0.56$  for females), so that rosette leaf number or size can be used as a convenient assay of total plant size. A significant sex  $\times$  half-sibship interaction was evident for the total dry weight associated with reproductive structures, indicating that patterns of genetic variation among half-sibships were not the same for the two sexes for this trait. It is interesting to note that among dry weight measurements, the only character that showed this significant interaction was associated with reproduction. The general trend which emerges from these data is that females have a more extensive root structure and a larger inflorescence structure. The most striking difference between males and females is in the quantity of resources that are committed to reproductive structures. The act of producing an inflorescence clearly represents a much greater drain on resources for a female than it does for a male.

One can use the dry weight measurements to assess the relative percentage costs of various plant parts (Figure 8-1). Females devote a significantly greater proportion of their resources to reproductive structures, whereas males have a significantly higher proportion of their resources in the rhizome and rosette leaves (Table 8-4). The percentage of the dry weight allocated to rosette leaves, rhizome, and roots showed significant variability among half-sibships. Hence these patterns of resource allocation are genetically variable for *C. luteum*. Aside from the sex-specific differences there appears to be no genetic variation for allocation to reproduction.

A significant sex  $\times$  half-sibship interaction was found for percentage dry weight in rhizomes, indicating that patterns of genetic variation for this trait were not the same

Table 8-3. Mean dry weight values for plants harvested in the phytotron experiment<sup>d</sup>

Character	Females	
	Males	Females
Rosette leaves	2.69	3.03
Rhizome	1.56	1.80
Roots	0.73	1.01
Reproductive structures	0.50	1.62

<sup>a</sup> Results of statistical contrasts on these data are presented in Table 8-4.

Table 8-4. ANOVA test results for mean dry weight and mean percentage allocation to various plant parts in Phytotron experiment

Source	d.f.	F ratios for dry weight <sup>a</sup>				F ratios for % allocation <sup>a</sup>			
		Rosette leaves	Rhizome	Roots	Reproductive structures	Rosette leaves	Rhizome	Roots	Reproductive structures
Sex	1	0.7 n.s.	1.9 n.s.	12.6 <sup>b</sup>	123.4 <sup>b</sup>	42.5 <sup>b</sup>	36.5 <sup>b</sup>	0.0 n.s.	154.2 <sup>b</sup>
Half-sibships within populations	16	1.8 n.s.	1.5 n.s.	2.3 <sup>c</sup>	2.5 <sup>d</sup>	2.6 <sup>d</sup>	2.1 <sup>c</sup>	3.0 <sup>b</sup>	1.6 n.s.
Sex $\times$ half-sibships within populations	16	1.1 n.s.	0.8 n.s.	1.4 n.s.	1.5 <sup>c</sup>	1.4 n.s.	2.0 <sup>c</sup>	0.9 n.s.	1.2 n.s.
Within populations									

<sup>a</sup> n.s., not significant.  
<sup>b</sup> p < 0.001.  
<sup>c</sup> p < 0.05.  
<sup>d</sup> p < 0.005.



Figure 8-1. Percentage dry weight allocated to various plant parts among flowering males and females raised under standard conditions. Results of statistical contrasts on these data are given in Table 8-4.

for males and females. If the rhizome serves in part as a storage organ for *C. luteum*, which is quite probable, then these differences between the sexes may result from the fact that flowering brings about a much greater resource depletion in females than in males. Under such circumstances, the storage organ would be expected to be subject to differential demands in the two sexes, which in turn might lead to genetic differences.

### Resource Allocation and Sexual Dimorphism in Natural Populations

The genetic differences between males and females in their life history characteristics as measured under standard conditions are also strongly evident in natural populations (Table 8-5; see also Meagher 1980, 1981, 1982, Meagher and Antonovics 1982).

Table 8-5. Life history characteristics of male and female plants measured in natural populations<sup>a</sup>

Site	Sex	Rosette N	leaf number	Mortality rates (% per year)	Percentage flowering in a given year
Natural Area	Males	2492	4.1	3.0	34
	Females	1014	4.4 <sup>b</sup>	2.6 n.s. <sup>c</sup>	13 <sup>b</sup>
Seawell	Males	1025	4.4	1.7	35
	Females	260	4.9 <sup>b</sup>	4.0 n.s. <sup>c</sup>	15 <sup>b</sup>
Silver Hill	Males	628	4.9	1.3	43
	Females	298	5.3 <sup>b</sup>	5.1 <sup>d</sup>	14 <sup>e</sup>

<sup>a</sup> Values presented are from 1975-1979 data pooled; cumulative numbers of observations (N) for each sex are shown. Statistical significance of male versus female comparisons are indicated by other notes. Rosette leaf numbers were compared using an ANOVA (Sokal and Rohlf 1969); mortality rates and percentage flowering were compared using a log-likelihood ratio (Bishop et al. 1975).

<sup>b</sup>  $p < 0.001$ .

<sup>c</sup> n.s., not significant.

<sup>d</sup>  $p < 0.01$ .

<sup>e</sup>  $p < 0.05$ .

Of the two sexes, females had a significantly higher number of rosette leaves in all three sites, and among plants in flower in a given year, a larger inflorescence as indicated by the number of inflorescence stalk leaves (Meagher and Antonovics 1982). The difference between males and females in annual mortality rate was not statistically significant in the Natural Area but it was so in the other two sites, with females having a higher mortality rate than males. Females therefore tended overall to have a higher mortality rate than males. Finally, females have a lower probability of being in flower in a particular year than do males and they tend to skip a greater number of years after flowering before they flower again (Meagher 1981, Meagher and Antonovics 1982). Consequently, females flower less frequently over a given span of years than do males.

Rosette size (number of rosette leaves) also appears to play an important role in determining the life history characteristics of males, females, and juveniles. Rosette size is highly correlated with inflorescence size for flowering individuals of both sexes and is also a good predictor of the change in size from one year to the next (Meagher and Antonovics 1982). Annual changes in rosette size are sex specific in that females tend to undergo more dramatic fluxes in size than males from year to year (Meagher and Antonovics 1982).

The rosette size of an individual is clearly a good assay of its life history status, as indicated by the correlations found between rosette size and dry weight indicated in the previous section and by the dependence upon size of most life history characters measured in the field. The change in rosette size observed in individuals with different flowering schedules therefore provides a reasonable assay of the drain on a plant's resources brought about by flowering as reflected in the individual's life history. The effects of flowering on rosette size transitions were assessed by considering 3-year size transitions of plants with different flowering schedules. The change in plant size from the year before to the year after flowering was estimated for plants that did not flower in year 1 or year 3 (Table 8-6). Plants did not fully recover their preflowering size by the end of the first year after flowering, and the net loss in size was significantly ( $p < 0.05$ ) greater for females than for males at all three sites.

The resource allocation patterns in the phytotron showed that flowering introduced a greater depletion of resources for females than for males. Demographic studies in the field on the impact of flowering on size and subsequent reproduction confirm that the additional drain on female resources has significant impact on the life history of females. In fact the differences between the two sexes have influenced their ecological tolerances such that males and females were differentially distributed into differing

Table 8-6. Percentage change in rosette leaf number from the year before to the year after flowering (year 3 - year 1)<sup>a</sup>

Site	Males		Females	
	n	(year 3 - year 1)	n	(year 3 - year 1)
Natural Area	247	-17	133	-39
Seawell	118	-16	34	-39
Silver Hill	28	+2	12	-34

<sup>a</sup> Statistical comparisons of males and females were all statistically significant ( $p < 0.05$ ), using t-tests (Sokal and Rohlf 1969).

ecological microhabitats within the Natural Area site (Meagher 1980). In the light of life history overall the female life history therefore can be seen as a result of selection favoring female plants that are buffered against this higher cost. In keeping with the predicted outcome of such past selective forces, females delay reproduction presumably until they can obtain a greater rosette size relative to males, providing them with a higher photosynthetic productivity and hence a greater ability to meet and recover from the resource demand of flowering. A tendency toward larger rosette sizes for females among plants in natural populations was also noted. For a given size of inflorescence, larger overall size would also result in a lower proportion of dry weight committed to reproductive structures.

The question remains why females should be constrained to produce a larger inflorescence rather than, for example, producing smaller inflorescences and flowering more often. One possible reason is that seed dispersal may be an important fitness component. Following the flowering season, female inflorescence stalks undergo a secondary elongation to almost double their height by the time seed are shed. There are no specialized mechanisms for seed dispersal (such as fleshy fruits or exploding seed capsules), and this additional elongation seems the only process that enhances seed dispersal in *C. luteum*. If this secondary elongation is a process that has evolved in response to selection for increased seed dispersal distances, then that may explain why females are constrained to produce such large inflorescences.

It has become strongly evident in the preceding sections that males and females are divergent in the manner in which their fitness is expressed through various components (Table 8-7). Males begin flowering younger and have a lower adult mortality rate so that they, on average, have a longer adult life span. Males also have a higher probability of being in flower in a given year. Females, in contrast, by virtue of the fact that they are in a numerical minority and by virtue of the fact that all male gametes passed on to the next generation must go via their seed production, have a much higher number of offspring produced per individual when they are in flower.

### Components of Fitness and Population Projection Models

The various components of fitness for males and females can be integrated into a demographic projection model to assess the long-term effects of sexual dimorphism in life history on population dynamics. Such a model is similar in principle to a modification of the Leslie (1945) model whereby the population is subdivided into stage classes rather than age classes (Lefkovich 1965). The matrix projection model considered here (Figure 8-2) distinguishes among the contributions of the juvenile, male,

Table 8-7. Relative importance of various components of fitness for males and females

Fitness component	Relative importance
Age of first reproduction	Males > females
Adult longevity	Males > females
Probability of flowering	Males > females
Genetic contribution to seedlings when in flower	Females > males

and female components of the population to overall population dynamics and, by extrapolation, to the intrinsic rate of increase of the population,  $r$ . A more detailed representation of this model, including size-specific effects, is given in Meagher (1982). For the sake of brevity, the model presented here does not include size-specific effects. There are a few minor discrepancies, therefore, between the presentation here and that in Meagher (1982) in values of  $r$  and in proportions of plants in different sex categories resulting from this difference, but the results are generally very similar.

The first row of the matrix in Figure 8-2 represents contributions of the various components of the population at time  $t$  to the juvenile component at  $t + 1$  and consists of (1) juvenile survivorship and the portion of the total seedlings attributed to juveniles that flowered for the first time at  $t$ , (2) the average contribution to seedlings at  $t + 1$  by males in flower at  $t$  multiplied by the probability that any given male would be in flower at time  $t$ , and (3) the average contribution to seedlings at  $t + 1$  by females in flower at  $t$  multiplied by the probability that any given female would be in flower at  $t$ . The male and female fecundities per flowering individual at  $t$  are assumed to be represented by half for each sex of the seedlings observed undergoing recruitment at  $t + 1$ . The portion of seedlings attributed to juveniles reaching sexual maturity based on the estimated proportion of plants in flower that were reaching sexual maturity (Meagher 1981, 1982). The second row of the matrix in Figure 8-2 represents contributions of each component at  $t$  to the male component at  $t + 1$  and includes (1) the probability that any given juvenile will flower for the first time as a male at  $t$  and (2) adult male survivorship. Similarly, the third row consists of (1) the probability that any given plant will flower for the first time as a female at  $t$  and (3) female survivorship. The third element of the second row and the second element of the third row represent the probabilities that an individual would undergo a sex change from female to male or male to female, respectively, and they are both equal to zero for this strictly dioecious species.

The differential effect of males and females on long-term projections can perhaps best be assessed by modifying the model to obtain a male-dominance model and a female-dominance model (Keyfitz 1977). This can easily be done for either sex by setting the contribution to seedlings from one sex equal to zero and doubling the contribution to seedlings by the other sex. The effect of this is to subsume the genetic contribution of the second sex into the genetic contribution of the first sex for pur-

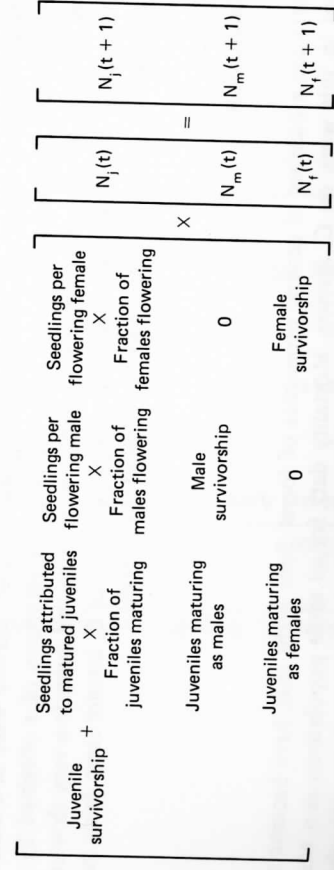


Figure 8-2. General demographic projection matrix for two sexes.

poses of population projection. One-sex projection matrices for *C. luteum* obtained in this manner (Table 8-8) do indicate a difference in the long-term effect of males vs. females. The female-dominance projections generally show a high intrinsic rate of increase than the male-dominance models, although the magnitudes of these differences are not very great.

A problem inherent in the types of projections conducted above is that they fail to take into account the possibility of interaction between males and females in the production of seedlings. Specifically, the relative magnitudes of contribution to seedlings per flowering male ( $C_m$ ) or per flowering female ( $C_f$ ) are generally calculated at the particular sex ratios prevailing in the populations at one point in time. If the populations were in a state of disequilibrium with respect to sex ratio at that point or if the sex ratios were undergoing continual perturbation in response to sexual selection, then the sex ratios of the populations will be changing over time as the populations approach equilibrium. Consequently, the true values of  $C_m$  and  $C_f$  will be different for the equilibrium populations, and the projections based on a  $C_m$  and  $C_f$  that stay constant over time irrespective of what is happening to the sex ratios will be distorted. In order to overcome this difficulty, a series of interactive models was generated (Table 8-9) in which  $C_m$  and  $C_f$  were calibrated to the new sex ratio as the sex ratio varied. Because the value of  $C_f$  for *C. luteum* appears to remain constant over the range of sex ratios observed in natural populations (Meagher 1980, 1982),  $C_f$  is assumed to remain constant, but  $C_m$  is free to vary as the sex ratio changes. In these projections, as each new matrix was generated  $C_m$  was adjusted to the predicted equilibrium sex ratio. This process was repeated iteratively until the matrices stabilized. Changes in  $r$  resulting from calibration of  $C_m$  also could influence the relative proportions as well as the overall proportions of juveniles maturing as males or females (Meagher 1982); this effect of proportion of juveniles maturing cannot be accounted for in the present projection because it is dependent on the precise distributions of ages at first reproduction in natural populations for both sexes, which are not yet known. However, estimates of  $r$  underwent negligible change in the present simulation, so that the initial estimates of proportions of juveniles maturing as males or females probably represent a reasonable approximation.

Estimates of  $r$  obtained using the interactive models differed only slightly from the estimates from male- and female-dominance models. A large departure in value between the estimates of  $r$  based on the two one-sex models would be an indication that the populations from which our estimates of  $C_m$  and  $C_f$  were derived were in a state of disequilibrium with respect to sex ratio. Because the estimates of  $r$  obtained by all three methods of projection are of very similar magnitude and indicate a very slow rate of increase in population size over time, the populations of *C. luteum* seem fairly near an equilibrium state with respect to overall life history traits.

## Conclusion

There are a number of general properties of forest floor herbs that have become evident in this work on *C. luteum*. Mortality data for all three populations as a whole indicate turnover rates that are relatively low and are hence consistent with observations on other forest floor herbs (Tamm 1956) in contrast to more recent reports of

Site	M	N	r	Males	Females	N	r
Natural Area	0.9107 0.0204 0.2859	0.0190 0.9660 0	0.0190 0.0204 0.9523	0 0 0	0.9660 0 0	0.4131 0 0.9667	0.047 17 16
Seawell	0.9269 0.0247 0.1128	0.0156 0.9824 0	0.0156 0.0247 0.9481	0 0 0	0.9824 0 0	0.2750 0 0.9566	0.018 36 51
Silver Hill	0.9222 0.0156 0.9857	0.9431 0 0	0.9793 0.0156 0.0192	0.059 0 0	0.9857 0 0	0.5924 0 0.9431	0.067 75 14

Table 8-8. Population projections for males and females

Site	N	M	Interactive model	Males only	Females only
Natural Area	65	0.2066	0.040	0.019	0.047
Seawall	48	0.0469	0.013	0.014	0.018
Silver Hill	71	0.2206	0.050	0.059	0.067

Table 8-9. Interactive projection matrices and stable population structures

turnover rates for other perennial plant species (see Hickman 1979 for review). However, these more recent studies have been concerned with the dynamics of populations exposed to extreme environmental conditions, such as mine spoils (Antonovics 1972) or ruderal "weedy" situations (Harper 1977, Sarukhan and Harper 1973, Werner 1975, Williams 1970). *Chamaelirium luteum*, however, is an understory herb in mesic mature hardwood forests; and, as such, it is not a transient or colonizing species. Individual plants within populations of *C. luteum* appear to be very long lived and may be as much a lasting part of the community structure of the forest as the trees with which they co-occur.

It is also clear for this dioecious species that differences between males and females in the nature of their contribution to sexual reproduction have far reaching impacts on their life histories (Figure 8-3). The higher "cost" of the female inflorescence stalk results in a much greater resource depletion for females as a consequence of flowering than is evident for males. This higher resource depletion quite probably exposes female plants to a higher risk of mortality as a consequence of flowering, which in turn would result in a higher selection intensity in females for larger plants with more leaf area and hence higher productivity that would help to buffer females against the additional resource depletion that they face. The larger inflorescence in females is believed to have evolved in response to other selection pressures, such as selection favoring increased seed dispersal by females, not measured in the present study. The overall pattern that emerges is that males and females are subject to different internal genetic constraints on resource allocation and that these differences in resource allocation are reflected in a wide spectrum of life history traits.

Even though males and females differed widely in terms of specific life history traits, the long-term projections based on male life history alone (male dominance) and

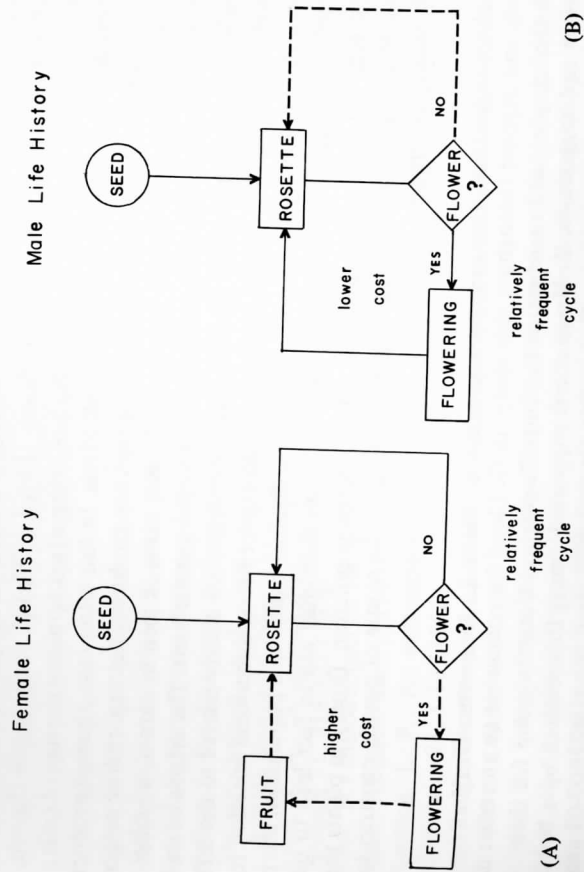


Figure 8-3. Life history overview for dioecious plant populations. (A) Female; (B) Male.

on female life history alone (female dominance) were really quite similar. It seems highly probable that although different components contribute to fitness of males as opposed to females, the net result in terms of overall individual fitness per male and per female are similar. This is not surprising in light of the fact that in any dioecious population the average fitness of the two sexes will be undergoing continual selection toward equality. In studying genetic differences in life histories of contrasting populations or species, these life histories may be the product of different intensities of selection or different constraints within individuals. In the case of dioecy, selection intensities will be similar in males and females because these two sexes make equal contributions to the progeny, and any differences in life history therefore serve to pinpoint the importance of internal constraints on the response to selection for life history traits. The results from the present study show that the constraints can have a large effect on two genotypes within one interbreeding population.

Because of the interdependence of male reproductive output and female reproductive output inherent in sexual reproduction, a population projection should consider the interaction of the two sexes. By studying the life histories of the two sexes separately and developing a projection model that considers relative contributions of both sexes, a more comprehensive understanding of the internal processes and differential nature of the contributions of males and females to overall population dynamics has been gained.

The importance of distinguishing between male and female contributions becomes even more evident in the general case for plants where both male and female functions take place in the same individual but to differing degrees among individuals (e.g., gynodioecy, polygamy; see Lloyd 1980 for discussion of gender states in plants). The relative importance of male and female fitness contributions (within the context of the total population) will determine individual fitness (Lloyd 1976). Furthermore, depending on the magnitude of conflicting constraints of male vs. female reproductive effort, there may be eventual evolution of dioecy (Lloyd 1979a) if, for example the sum of male and female fitness for two individuals of different sex surpasses the sum of male and female fitness of two hermaphroditic individuals. In this latter case, a parent producing dioecious progeny will have greater fitness than one producing hermaphroditic progeny.

The differences in the life history of the two sexes as seen in natural populations was shown in the phytotron studies to have a clear genetic basis. The origins of such a marked genetic dimorphism within a single population are clearly related to the differences in sex function. Even though one would expect strong directional selection for a particular life history that would maximize individual fitness in a population, internal genetic constraints resulting from sexuality of an individual can in fact lead to quite divergent life history variation even within a single population. Dioecy in plants therefore serves as a model system to gain insight into the nature of genetic constraints on life history evolution.

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