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ECOLOGICAL CONSEQUENCES OF DIOECISM IN PLANTS:
A CASE STUDY OF SEX DIFFERENCES, SEX RATIOS
AND POPULATION DYNAMICS OF VALERIANA EDULIS NUTT.

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Judith Dingle Soule

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Patricia A. Werner
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By

Judith Dingle Soule

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ABSTRACT

ECOLOGICAL CONSEQUENCES OF DIOECISM IN PLANTS: A CASE STUDY OF SEX DIFFERENCES, SEX RATIOS AND POPULATION DYNAMICS OF VALERIANA EDULIS NUTT.

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Dioecism, the condition of separate sexes, has certain unique ecological consequences which can influence its evolution or maintenance. Consequences to sexual specialization, outcrossing, pollination, colonization and spatial distribution of pollen and seeds are reviewed in terms of potential positive or negative effect on individual fitness. Emphasis is placed on the potential for sexual specialization to influence the evolution of dioecy. Sexual specialization in one perennial dioecious species, *Valeriana edulis*, was explored in field studies. Growth, survival, and flowering of over 600 marked plants were monitored for three years in four populations to compare male and female life history characteristics for this species.

First, the hypothesis that male reproductive effort (RE) is lower than female was explored. Then resource allocation differences between the sexes, expected to follow from RE differences, were examined. Males of *Valeriana edulis* did allocate a lower proportion of annually renewed biomass to reproduction each time they flowered than did females. Males also flowered more frequently than females, but still, average male RE per year was lower than female. Males first became reproductively mature at smaller sizes than females, but males and females did not differ in average annual growth rate or survival across the four populations.

Differences between the sexes have consequences to population dynamics and adult sex ratio. Four populations of *Valeriana edulis* with different adult sex ratios were used to compare effects of sex differences in size at maturity, flowering frequency, and survival on sex ratio. Adult sex ratio was always female-biased, ranging from 29% to 46% male, with a mean of 38%. Survival differences between the sexes, though not significant when the populations were combined, were correlated with adult sex ratio when each population was examined separately. Differences between the sexes in size at maturity had little effect on adult sex ratio because populations were dominated by older plants. Higher male flowering frequency was masked by the female bias in sex ratio so that sex ratio among flowering plants was only slightly less female-biased than sex ratio among all adults, flowering and resting. Indications were found that sex ratio is also female-biased prior to adulthood.

A size-stage projection matrix population dynamics model was developed to explore the population dynamics of *Valeriana edulis* using data from the field studies. Consistent with the life history of *V. edulis*, three of the four populations appeared to be near stable population size; the fourth was declining. When female survival was higher than male, population growth rate was higher than when survival of the sexes was equalized (same average rate). Observed adult growth and survival rates of males and females produced female-biased adult sex ratios at equilibrium, starting with a primary sex ratio of either 50% or 35% male. The model predicted that at equilibrium, an average male would father two to four times as many seeds as an average female produces each year.

To my father...

for teaching me to answer my own questions

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CHAPTER 1

ECOLOGICAL CONSEQUENCES OF DIOECISM IN PLANTS

INTRODUCTION

Dioecism, the condition of separate sexes, has apparently arisen secondarily from bisexual breeding systems independently a number of times in widely scattered taxa and in a variety of life forms, yet is rare in higher plants (Darwin, 1876; Yampolsky and Yampolsky, 1922; Lewis, 1942; Westergaard, 1958). One dilemma which arises in attempts to discern selective advantages of dioecism over bisexuality in plants is that unless seed production in females (or pollen in males) doubles compared to bisexuals, a parent producing dioecious offspring loses up to half its reproductive potential over a parent producing bisexual offspring (Lewis, 1941). To understand the evolution of dioecy one needs not only to find some advantage of this breeding system, but an advantage that more than makes up for the inherent 50% cost of a simple switch to single sex function.

While complete reproductive compensation (e.g. doubled seed output) may be expected theoretically via reallocation of resources previously devoted to the opposite sex function, in plants where dioecism arises from bisexuals (Charnov et al., 1976) such compensation requires a much more complex set of linked mutations than a simple gene for sterility of one sex. Further, it is not clear that the amount of resources devoted to pollen is necessarily equal to that devoted to ovules in a bisexual plant, so that complete compensation is not necessarily even possible given a switch to unisexuality. Smith and Evenson (1978) found a considerably lower proportion of biomass allocated to anthers and pollen than to female structures in hermaphrodite flowers of _Amaryllis_ spp. Self compatible species generally spend less on pollen relative to ovules than do self-incompatible species (Cruden, 1977; Lemen, 1980) suggesting that less than equal effort is invested in pollen in self-compatible species. Primack and Lloyd's (1980) studies on distribution of gender showed not only variation in gender expression (the amount of contribution via pollen or ovules) among individuals of self-compatible species, but also variation in gender in self-incompatible species. This also suggests that equal investment in male and female function is not universal. Freeman et al. (1980) found extreme variation in the number of male and female flowers in monoecious species, such that some individuals or populations invested much more in one sex or the other. Horovitz (1978) recently questioned on theoretical grounds the equisexuality of hermaphrodites even in outcrossing species. Differences in relative male and female function among individuals within a population may facilitate co-evolution of unisexuality and higher reproductive output, but may also tend to limit the degree of reproductive compensation possible.

Several advantages of dioecism have been hypothesized for specific taxa, or groups of dioecious species (the most popular is enforced outcrossing; see Bawa, 1980 for a review of these), this approach ignores potential disadvantages which are inherent to dioecism (beyond the 50% cost of unisexuality). Rather than postulating possible advantages of dioecism under particular situations, it may be more enlightening at this point to examine the general ecological consequences of dioecism in plants. In other words I will take the approach, that given dioecy arises, what are the ecological consequences, how does each consequence affect individual fitness, and what effect do other life history traits have on the realization of each consequence. Some consequences are negative in effect on fitness, some positive; some are unique to dioecism compared to other breeding systems. By this approach it should be possible to prepare a balance sheet of positive and negative fitness effects for the several unique consequences of dioecy. In this way, selective forces which have predominated in particular situations in order for dioecy to evole and be maintained can be defined. It is likely that from this approach several suites of life history traits will emerge which could facilitate the evolution of dioecism by enhancing positive and minimizing negative consequences. The greatest value in this approach is that it unites the evolution of breeding system with other aspects of ecology and life history.

Here I will discuss in detail ecological consequences of dioecism compared to other breeding systems in plants, and point out life history characteristics which minimize disadvantages or maximize advantages.

Consequences to Sexual Specialization

The genotypes of dioecious plants which produce pollen are distinct from those which produce ovules (excluding those cases of phenotypically plastic sex determination). Therefore selection operates somewhat independently on pollen and ovule producers and it is possible for males and females to diverge ecologically, each specializing in a manner that optimizes their respective reproductive roles. Once dioecy evolves, and individual plants are no longer constrained by the sex-related requirements of the opposite sex, sexual divergence may occur, whether or not it is adaptive compared to other breeding systems. As long as divergence of the sexes occurs after the acquisition of dioecism, it will not influence the evolution of dioecism, but could be significant in the maintenance of dioecy. An alternative view holds that some aspects of sexual divergence may be immediate enough in effect to present a selective advantage or disadvantage compared to individuals with other breeding systems, and thus influence the evolution of dioecy (Willson, 1979). By looking at specific ways the sexes may diverge and examining positive and negative effects relative to being non-divergent, the difference between these two viewpoints may be resolved.

The forms of divergence can be organized by what part of the reproductive strategy differs between the sexes: 1) reproductive expenses - when these differ between sexes, divergence in resource allocation schemes is possible; 2) timing of reproductive expenditure - when this differs, phenology of events other than flowering may differ for the sexes. Either of these differences can also lead to divergence of habitat utilization by the sexes. Lloyd and Webb (1977) have recently published a thorough and extensive review of secondary sexual differences in plants which emphasizes patterns of occurrence and hypothesizes bases of sexual differences. Therefore I will not attempt to duplicate their literature review, and will limit this discussion to certain ecological aspects of sexual divergence which may affect maintenance or evolution of dioecy.

Reproductive Expenses: Female reproductive expenses include production of flowers, reception of pollen, nourishment of immature seeds, protection of seeds, seed dispersal. Male reproductive expenses include production of flowers and dispersal of pollen. It would seem that male expenses per reproductive season would usually be less than those of females (Freeman et al., 1976; Lloyd and Webb, 1977). Putwain and Harper (1972) obtained a crude estimate of reproductive expense per flowering episode for male and female *Rumex acetosella* and found that females invested more calories in reproductive structures and products than did males. In the three other dioecious species for which similar data is available, male reproductive effort is lower than female as long as minimal seed set occurs in females (Wallace and Rundell, 1979; Hancock and Bringhurst, 1980; Gross and Soule, 1981). If this is generally true, it is also possible that males allocate resources to other functions differently than females on a seasonal, or lifetime basis.

During the period of seed maturation for females, males of species with cloning ability should be able to invest more effort into vegetative propagation than females because males' sexual reproductive effort termiantes with the end of the flowering period. In this situation males would have a higher potential for vegetative spread than females (Opler et al., 1975, Lloyd and Webb, 1977). Some evidence supports this. Males of *Fragaria vesca* in gardens produce many runners and may overrun females, which produce few (Darwin, 1868 and 1877). In *Rumex acetosella*, male shoots outnumber female shoots after reproductive maturity is reached, and males allocate proportionately more resources to vegetative propagation than do females (Putwain and Harper, 1972). In contrast, Hancock and Bringhurst (1980) found no difference in vegetative propagation in males and females of *Fragaria chiloensis*, even though female reproductive allocation was higher than male.

If this divergence occurred early in the evolution of dioecy, for instance as a plastic phenotypic change in resource allocation scheme in newly male (female-sterile) plants, these more vegetatively aggressive males would have an advantage over bisexuals. This would immediately affect individual fitness of males, indpendent of their frequency. There is a logical problem in attributing a role in maintenance or evolution of dioecism to such an advantage: ultimately this trait leads to males overrunning or out-competing females. This would not benefit long-term fitness of either sex, and would tend to constrain the amount of divergence in vegetative propagation occurring in dioecious species.

Other differences in resource allocation schemes are also possible given lower reproductive effort by males. Males could devote more resources to growth than females, leading to a faster annual growth rate for males than females once reproductive age was attained. Males could also allocate more resources to storage organs than females, increasing survival ability. One would not be surprised then to find males larger, or hardier than females. Greater winter hardiness and growth rates of males have been reported for Russian trees (Soroka, 1974; Lysova and Khizhnyak, 1975; Sizov, 1975). In contrast, females of *Populus tremuloides* have higher annual growth rates than males (Grant and Mitton, 1979). Differences in properties of wood between sexes of willows (Warren-Wren, 1972) may also indicate different growth rates, although it is not clear which sex grows faster. In several dioecious species of Umbellifereae of New Zealand, the sex ratio of reproductive adults is increasingly skewed towards males as size or age increases (Lloyd, 1972). (See also, Dzhaparidze, 1967, and Lloyd and Webb, 1977 for many other examples of male-female differences in dioecious plant species.)

Potentially, any of these forms of divergence are immmediate consequences of shifts in resource allocation from seeds to other functions in a new mutant male, thus giving an immediate advantage over a bisexual plant. However, the apparent inferiority of females in these cases, indicates that similar benefits are not gained by becoming a unisexual female. Thus, it is hard to imagine that these could be the primary impetus for the evolution of dioecism as suggested by Willson (1979). It seems more likely that the sexes diverged in some traits after dioecism was already established.

Timing of Reproductive Expenditure: Differences in the annual phenology of males and females (particularly post-flowering phenology) are expected because of differences in the length of time of reproductive expenditure (Putwain and Harper, 1972; Lloyd and Webb, 1977; Gross and Soule, 1981). Females must retain an infloresence past flowering (until after seed dispersal), while males need not. Thus, males have the option of moving on to death (in annual species), or a winter dormant state (in temperate zone perennials), or more vegetative growth, sooner than females. Males of *Rumex acetosella* (a perennial species) begin spring growth earlier and senesce earlier than females (Putwain and Harper, 1972). In males of perennial dioecious species of

Umbelliferare, the huge inflorescence quickly collapses and withers post-flowering, but females maintain the inflorescence alive and erect for several weeks longer (Lloyd, 1973). Male inflorescences of the dioecious perennial lily, _Chamaelirium luteum_, wither soon after flower production in the spring, but female inflorescences elongate and are maintained until seed dispersal occurs later in the season (Meagher and Antonovics, 1981).

During the period when only females are involved in reproduction, males and females should react differently to selective pressure, since they are experiencing different sets of resource demands. For instance, in cases where a limited resource such as water becomes more limiting as the season progresses, differences in water use by males and females could significantly affect average fitness. While female water use remained high throughout seed maturation, male water consumption could drop when inflorescences senesced, leaving more total water available for females. Bisexual plants would have lower average water availability, because all individuals would maintain inflorescences until seed dispersal. This may appear to be a group-selection argument when merely presented as an advantage of dioecism over other breeding systems. Actually, such a purported advantage could not positively influence the evolution of dioecism. It is, not only dependent upon a certain minimum frequency of new unisexuals in a population where these new mutants appeared, but would also benefit the bisexuals present as much as the new unisexuals. However, once dioecism was already fixed in a population, this form of divergence would be advantageous to all individuals, and thus could aid in the maintenance of dioecism. Early senescence of inflorescences would benefit perennial males by reducing resource stress (e.g. water). Females would benefit from greater resource availability. Thus, individual selection could result in this type of divergence post-evolution of dioecy.

Divergence in habitat utilization is another possible result of sexual differences in either timing of reproductive expenditure and/or amount of reproductive expenses. By dying back, dropping leaves, and/or becoming winter-dormant, perennial males could potentially occupy particular microsites that become poor in resurces or very stressful after the flowering period. Females may not have this option because they must mature fruits, and therefore they may be confined to "better" microsites. Thus males and females have the potential for occupying a different range of microhabitats (Freeman et al., 1980). In a study of five dioecious wind-pollinated species (Freeman et al., 1976) females were more common than males in moister areas and *vice versa*. The authors hypothesize that early in the season when pollination occurs water is not severely limiting in either dry or moist areas, but it becomes more scarce (especially in the dry areas) as the season progresses and as seed ripening occurs on females. It appears that due to different male-female phenologies in reproductive expenditure, males are successful in areas where females are not.

Again, it is difficult to see how such divergence, if it occurred simultaneously with a mutation for unisexuality, could promote the evolution of dioecy. Even though the unisexual's male progeny could survive over a broader range than the bisexual, in the shared, "better" portion of the habitat, a unisexual female would have no *a priori* advantage over the bisexual. Further, the dioecious plant probably would suffer the loss of female offspring which were dispersed to sites where only males could survive. Note that in this case, phenotypic sex determination (cued by environmental factors) would greatly improve the evolutionary picture for dioecy, since it could eliminate this seed loss (Freeman et al., 1976; Charnov and Bull, 1977).

On the whole, sexual specialization probably has little influence on the evolution of dioecism, but dioecy, once evolved, sets the stage for possible, secondary sexual divergence. In turn, such divergence effects other aspects of the ecology of the species, and potentially, the maintenance of dioecy.

Consequences to Outcrossing

Dioecy insures obligate outcrossing, and this is often considered the most important consequence of dioecism (e.g., Lewis, 1942; Baker, 1959; Dawson, 1964; Carlquist, 1966; Heslop-Harrison, 1972; Lloyd, 1972; Bawa and Opler, 1975). Self-incompatible hermaphrodites and possibly "temporally dioecious" (Cruden and Hermann-Parker, 1977) species share this feature, whereas in other breeding systems, at least a possibility of self-pollination exists. Out-crossing has generally been considered to be a positive feature because it helps produce genetically variable offspring and reduces the possibility of inbreeding depression. However, it may be considered disadvantageous to have no flexibility in level of outcrossing *versus* selfing (Lewis, 1942; Bawa, 1974). This lack of flexibility is at the root of the problem of colonization for a dioecious species, discussed below.

It is difficult to accept the idea that the advantage of obligate out-crossing lies solely in promoting genetic variability, because obligate out-crossing alone does not necessarily maximize genetic variation (stated also by Willson, 1979). Inbreeding among close relatives is not affected by a mere switch from self-compatibility to dioecy; the degree of genetic variability among offspring depends on the amount of inbreeding, seed dispersal, pollen dispersal, and establishment patterns (Grant, 1975). Although inter-individual pollination is insured by dioecism, the nature of dioecism actually reduces the number of potential mates, and tends to reduce overlap of seed dispersal patterns from different parents (see below). Both of these effects would increase the probability of breeding with close relatives compared to bisexual populations. The interplay of all these effects determines the relative degree of inbreeding with dioecism, compared to a bisexual breeding system. If suitable species pairs were found, a study of neighborhood size (Levin and Kerster, 1971) in dioecious and nondioecious species pairs might be enlightening.

Another postulated advantage of obligate outcrossing is to prevent inbreeding depression occurring because of self-pollination (Cruden and Hermann-Parker, 1977; Charlesworth and Charlesworth, 1978a and b). Inbreeding depression generally occurs only when populations which have long been out-breeding are then inbred (Wright, 1977). Outbred (and hence out-crossed) populations may have accumulated recessive lethal mutations that are expressed upon inbreeding. However, habitually inbred species do not show similar depression (Wright, 1977). Thus selection (i.e., inbreeding depression) operates against selfing only in normally non-selfing species. Charlesworth and Charlesworth (1978a) argue that there is some evidence of inbreeding disadvantage in partially selfed species, and suggest that dioecy will most likely evolve in such species, in response to some situation allowing inbreeding depression to become severe. Whether the original line is wholly outcrossing or partially selfing, the following scenario for the evolution of dioecy is provided: an effective outcrossing system (other than dioecy) in a population begins to break down (due to a change in some extrinsic factor), selfing occurs, inbreeding depression results, and dioecy is favored since it prevents selfing. Now let us consider the likelihood of this occurrence with examples of possible original outcrossing systems.

If the original outcrossing system consisted of a tightly coevolved pollinator and a special floral morphology, a loss of this pollinator could increase the incidence of selfing. It is likely, however, that it would also decrease pollination effectiveness, and dioecy would only further reduce the effectiveness, due to the fact that only 1/4 of interplant moves are correct with dioecy (male to female). This inefficiency due to dioecy would have to be significantly less than the effect of inbreeding depression for dioecy to be selected under these circumstances. This is not to say that it would never occur, however. In fact, Ornduff (1966) proposed exactly this scenario for the evolution of dioecism from distylous taxa. Recently, Beach and Bawa (1980) outlined the particular change in pollinators that appears to have occurred in several distylous groups where dioecy has arisen. They also presented data that demonstrated both reduced pollination efficiency and fertility in cases where this change in pollinators occurred. This appears to be a strong case where dioecy evolved as a direct result of an out-crossing system breaking down. It seems probable that prevention of inbreeding depression was the advantage of dioecy here.

On the other hand, if the original out-crossing system was physiological self-incompatibility, a simple breakdown in that incompatibility system would be unlikely to result in a switch to dioecy. Evolution of dioecy would be a very major change, involving a switch from a physiological to a morphological system. Where the original out-crossing system involved temporal separation in the sexual expression of individuals (temporal dioecy, or dichogamy), breakdown might be caused by a change in cues triggering development of each sex, e.g., a shift in climate or altitude. Here, as in distyly, selection for dioecy is not unreasonable because sexes are already developmentally separate (Darwin, 1877).

Increased genetic variability of offspring, and reduction of inbreeding depression are both immediate effects of the obligate out-crossing which is a consequence of dioecism. Thus, either can affect the evolution of dioecism.

Consequences to Pollination

In a hermaphordite species, all interplant moves made by an animal pollen vector have the potential to result in pollination. In a dioecious species, however, only one out of the four possible types of interplant moves (the move from a male to a female) has this potential (Ghiselin, 1974). Even gynodioecious species (species with some plants female, some hermaphroditic) have a higher potential than dioecious species - two of the three may succeed. A dioecious mutant in a hermaphrodite population will not experience a decrease in return rate immediately; rather, the inefficiency increases as the proportion of single-sexed individuals in the population increases. Because in this case dioecy is increasingly disadvantageous, adaptations which counteract the lowered pollination return rate should be favored.

One possible counteracting adaptation which should be favored is an increase in the average pollen production per male (without a concurrent increase in ovules per female). Increased pollen production could raise pollination effectiveness, but at the same time would raise the investment of resources into pollen, and thus, the cost of reproduction. Selection should seek a balance between these opposing pressures. Nevertheless, I predict that the pollen to ovule ratio will increase in populations where dioecy is becoming fixed.

Plants can minimize the decline in number of accomplished fertilizations which occur as dioecy becomes fixed by increasing the number of interplant moves made by pollinators. Even though the percentage of successful moves would drop as dioecy went to fixation, the absolute number of correct moves could remain constant if more interplant moves occurred. Therefore, the effectiveness of pollination would not decline (despite a decline in efficiency). Thus, increased pollen production co-occurring with dioecy would include, both a benefit (maintainence of pollination effectivness) and a cost (wasted pollen and other vector rewards on ineffective moves). One way to increase interplant moves by pollinators is to decrease the number of flowers per plant open at one time, encouraging shorter visits per plant. However, decreased attractiveness of a smaller floral display might well counteract this effect. Further, if the plant's pollinators tend to visit only one to a few blossoms per plant anyway, reduced number of blossoms would not be effective. Another such adaptation is a condition where male plants open their flowers earlier in the day than do females. By the time females open, males should be less attractive (nectar depleted, pollen gathered) and so many vectors should move from the males to the females (Bawa and Opler, 1975). This situation could insure more moves from male to female than in a case where both sexes open at the same time, but would require that pollen stay viable and attached to the vector for considerable time after leaving the male flowers.

Some published studies suggest that these types of adaptations do occur. Although I know of no data on pollen/ovule or flowers/plant ratios which compare closely related dioecious and nondioecious species, out-crossing species in general have much higher pollen/ovule ratios than species with some degree of selfing (Cruden, 1977). Dioecious species of *Amaranthus* have greater anther volume, though similar weight in seeds than monoecious species (Lemen, 1980) suggesting higher pollen/ovule ratios for the dioecious species. Bawa and Opler (1975) reported that for some dioecious tropical forest trees, flowers on male trees open in the morning, while female flowers open in the afternoon. Presumably, many vectors switch from males to females when the latter open. In this particular study, the pollination inefficiency imposed by dioecism might be expected to be especially significant since the trees have many small flowers open at once, and their pollinators are small unspecialized insects. Inter-tree moves would likely be fairly infrequent without the timing difference, each insect saturating on a small part of one tree. Bawa and Opler pointed out that a dioecious species has an advantage over a self-incompatible hermaphrodite in this situation, because the latter would suffer from clogging of stigmas with its own incompatible pollen.

An analogous situation to the tropical trees may occur among dioecious species with extensive vegetative reproduction ("cloners"). The potentially large number of blossoms per individual genet in cloners invites pollinator satiation on one individual plant. One might expect daily separation of flowering times between sexes in cloning dioecious species. To my knowledge no relevant data are available.

In some respects wind-pollinated dioecious species face the same problem as animal-pollinated species: a lower probability of successful pollination, since pollen intercepted by male plants has essentially made a "wrong move". Wherease animal pollinated dioecious species may experience enhanced pollination efficiency by daily separation of the flowering times of males and females, wind pollinated species might best enhance pollination by spatial segregation of the sexes (Freeman et al., 1980). Providing reliable wind current patterns were exploited by an arrangement in which males were locally upwind of females, or in which males were in updraft areas and females in dead spots where pollen tended to settle out, pollination would be facilitated. Although the pollination inefficiency of dioecy could be avoided by wind-pollinated species with such an arrangement, mortality during sorting of seedlings would be the "cost" to those species.

A recent study in Utah (Freeman et al., 1976) of five dioecious wind-pollinated species revealed some spatial segregation between sexes. In all species, males occupied the drier slopes and exposed areas in greater abundance than females, which were more abundant in wetter spots than were males. The authors suggested that these areas correspond to windy and protected areas, respectively. Freeman et al. (1980) document a significant correlation between percentage dioecism and percentage wind pollination in plant communities of North America, not inconsistent with the view that wind-pollination may be conducive to the evolution of dioecism (Darwin, 1877; Grant, 1958; Stebbins, 1951; Baker, 1959; Carlquist, 1966).

In both the animal-pollinated tropical trees discussed earlier, and the case of wind-pollinated plants, at least some benefits would be realized immediately by an individual unisexual mutant. Females in the former case would immediately cease to have stigmas clogged by self pollen. Males in the latter case would immediately benefit from higher probability of pollen dispersal. However, males of animal-pollinated, and females of the wind-pollinated species would seem to benefit only as frequency of unisexuality increased.

Consequences to Colonization

In order for a dioecious species to colonize a new site, the "effective propagule" is one male and one female seed (Baker, 1959). The probability of this combination arriving is only half the probability of any two propagules (the effective propagule of a self-incompatible hermaphrodite), and only one quarter that of a single seed (the effective propagule of a self-compatible hermaphrodite). Thus, an individual plant which produces dioecious offspring has a lower probability than a hermaphrodite of having offspring successfully colonize and establish a new population on a new site (Fryxell, 1957; Williams, 1975). This lower ability to colonize new sites would be a significant loss in fitness only for a species where such colonization episodes were frequent, of course. It is perhaps not surprising then, that dioecious species tend to be woody and long-lived (Darwin, 1876; Baker 1959; Bawa and Opler, 1975; Freeman et al., 1980), and that few dioecious species are herbaceous, the most common habit of colonizing species.

In contrast to the effects on pollination discussed above, reduced colonizing ability of offspring immediately lowers the fitness of dioecious individuals of either sex, relative to bisexual forms, and is not dependent on the frequency of unisexuals in a population where dioecy has arisen. Thus, if colonization of new sites were an important life history phase of a species, one would not expect dioecism to be selected.

I suggest that if dioecy and weediness co-occur in the same species, it is in taxonomic groups where some related species are dioecious, but not weedy (suggesting an ancestry of dioecy, and more recent acquisition of weediness), rather than where relatives are weedy, but not dioecious (suggesting an ancestry of weediness, later aquisition of dioecy). I surveyed two of the genera containing a number of weedy and dioecious species, Rumex and Silene, in this light. In Rumex, weediness is scattered throughout the genus, but dioecy is confined to two small subgenera, suggesting that dioecy came first and weediness second (using data from Trelease, 1892; Small, 1903; Britton and Brown, 1913; Munz and Keck, 1965; Tutin et al., 1964, 1968, 1972, 1976). In Silene it also appears that lines of dioecious species developed, and some time later, some of these developed weedy habits. For example, the European subgenus Otities Otth., is dominated by nondioecious species, of which about 40% are weedy, while only one out of nine dioecious species is weedy (Tutin et al., 1976). It would be useful to do more detailed systematic surveys on these and other groups with both dioecious and weedy taxa.

Certain adaptations which enhanced colonizing ability of a dioecious species independent of breeding system, would increase the chance of a dioecious species evolving a colonizing life history. For example, first consider a type of adaptation which increased the probability of two seeds landing together. A simple mechanism is dispersal of seeds in groups from the parent (Carlquist, 1966), e.g., by a multi-seeded fruit instead of an individual seed. (This would also increase chances of inbreeding among offspring in a new site, which itself would have an unknown effect on fitness). A second adaptation is seed dormancy with local dispersal of seeds. This combination of characters could give a pattern of repeated colonizations of the same site, with no adults present for some period of time between colonizations. This holds little risk for a dioecious species because many seeds may break dormancy simulataneously, providing a number of potential mates. Another adaptation which would counteract the lower probability of long distance colonization conferred by dioecy, is asexual reproduction (apomixy) or vegetative propagation. Either of these traits allows one offspring to fill a site with copies of itself and hold it for a long time. Instead of insuring that mates will be present when and where offspring germinate, this strategy depends on an individual holding a large enough site long enough to mate eventually with another member of its species.

A survey of the literature demonstrates that these adaptations do co-occur with dioecism. Dioecism and apomixis reportedly co-occur commonly in species (Gustafsson, 1946), the most extreme case being the genus Antennaria which is wholly dioecious and has widespread apomixis (Lewis, 1942). As for vegetative propagation, I compiled data from several floras on the capacity for vegetative propagation among dioecious species and their non-dioecious relatives (Table 1-1). Only groups with some members with both dioecism and vegetative propagation were included. The percentage of species with vegetative propagation was computed for the dioecious and for the nondioecious categories of each taxonomic group. These percentages were then compared across all groups by means of a Wilcoxon Signed Rank test. This analysis revealed that more of the dioecious species could propagate vegetatively than their nondioecious relatives.

It should be noted that this analysis weights each taxonomic group equally, rather than weighting each species equally. Since the point of the survey was to show whether an overall trend in evolution of vegetative propagation in dioecious taxa exists, the taxonomic groupings are the logical replicates, not the species, for the following reason: any consideration of species gave inordinate weight to those groups in which speciation has been the greatest. However, even if species are dealt with equally, a chi-square test shows the same result for the three floras combined.

Adaptations that counteract the relatively poor colonization ability conferred by dioecism may be the key to success of the few species that are dioecious and successful weeds (e.g., Silene alba and Rumex acetosella). Silene alba, colonizes new sites when seeds are mixed into agricultural crop seeds (McNeill, 1977), a mechanism which provides excellent dispersal of seeds in groups. Natural dispersal may

Table 1-1: Frequency* of vegetative reproduction in dioecious and non-dioecious members of selected herbaceous taxa from the floras of New Zealand, USSR, and Japan**. (Herbaceous taxa in which no members reproduce vegetatively are not included.)

Taxon	DIOECIOUS Number		DIOECIOUS % with Vegetative Reproduction		NOT DIOECIOUS Number		NOT DIOECIOUS % with Vegetative Reproduction	
	genera	/species	genera	/species	genera	/species	genera	/species
NEW ZEALAND								
Family Compositae								
Tribe Antemideae	1	7	100	86	3	27	67	55
Family Umbellifereae	2	44	100	11	12	48	58	85
Family Zannichelliaceae	1	1	100	100	1	1	100	100
Family Liliaceae	3	17	67	65	6	10	67	50
USSR								
Family Cyperaceae								
Subfamily Cariocideae	1	8	100	100	2	392	100	80
Family Liliaceae								
Subfamily Asparagoideae	1	4	100	100	11	58	?50	?50
Family Ploygonaceae								
Genus Rumex	(1)	5	(100)	40	(1)	44	(100)	2
Family Rosaceae								
Subfamily Spiraceoideae	-	6	-	17	-	32	-	3
Subfamily Pomoideae								
Tribe Potentilleae	-	10	-	60	-	233	-	19

Table 1-1, continued

	DIOECIOUS				NOT DIOECIOUS			
Taxon	Number		% with Vegetative Reproduction		Number		% with Vegetative Reproduction	
	genera/species		genera/species		genera/species		genera/species	
Family Euphorbiaceae								
(herb. g. only)	1	3	100	67	6	177	17	13
Family Umbelliferae								
Tribe Amnineae	2	9	0	0	46	254	-	4
JAPAN								
Family Gramineae	1	1	0	0	99	278	-	51
Family Hydrocharitaceae	3	6	67	83	4	7	0	0
Family Compositae	4	7	-	86	68	340	-	22
Family Cucurbitaceae	1	1	0	0	5	10	20	10
Family Liliaceae	5	18	-	50	38	148	-	39
Family Polygonaceae	2	8	100	100	3	57	67	17

* Using the Wilcoxon Signed Rank Test for differences on this data, (column 4 - column 8), it was found that percentage dioecious species with vegetative reproduction is significantly greater ($P<0.05$) than percentage non-dioecious species with vegetative reproduction.

** Allan, 1961; Moore and Edgar, 1970; Komorov, 1934; Ohwi, 1965.

also tend to be in groups, because seeds are contained in capsules which tend to deposit seeds in groups. *Rumex acetosella* has a great capacity for vegetative propagation, and in some situations populations may be maintained by vegetative propagation alone (Putwain and Harper, 1972, and references therein). Dioecious taxa on islands, some of which were probably dioecious at the time colonization occurred (Carlquist, 1966), may also be expected to show adaptations for colonizing ability.

Consequences to Physical Distribution of Pollen and Seeds

The density of females of a dioecious population is only one half the density of the total adult population (geven random dispersion of the sexes and a 1:1 ratio of males to females). This means that points of seed production and dispersal are on the average farther apart in a dioecious population than in an equally dense hermaphrodite (or monoecious or gynodioecious) population. This population attribute actually affects individual fitness in several ways, some directly and immediately and some dependent on the frequency of single-sex individuals in a population.

For a male, on the average there are fewer ovule-bearing plants within any given radius of that male in a dioecious than in a hermaphrodite population of equal density. This reduces the average number of mates available to a male in a dioecious compared to an equally dense population of bisexuaqls. It is important to note that while dioecism may inforce out-crossing, it also reduces the number of combinations of matings occurring, thereby reducing the out-breeding potential.

For a male of a wind-pollinated species, the volume of pollen reaching a particular point is a function of the male's distance from that point; the amount of pollen delivered to a point decreases exponentially as the distance increases (Levin and Kerster, 1974). If dioecy is being selected in a population (due to other factors) the amount of a male's pollen reaching ovule-bearing plants will decrease, given no change in density. In dioecious wind-pollinated Amaranthus altissima, the level of fertilization was only 12% in a low density population, compared to 81% in a high density population. In contrast, in monoecious Amaranthus species, in which self-fertilization was possible, fertilization levels did not respond to density (Lemen, 1980).

This consequence of dioecism will not represent a disadvantage for a dioecious male compared to a pollen producing bisexual in the same population, because the bisexual will be faced with the same distribution of ovule-bearing plants as the male (assuming that bisexuals, males and females are intermixed). Nevertheless, a male might be favored which could somehow counteract the effect on fitness of this decreased availability of mates. The simplest ways to do this are to increase pollen dispersal distance, and/or to increase the amount of pollen produced. For a wind pollinated species the former could be accomplished by making more bouyant pollen, or possibly, only releasing it in high winds. For an insect-pollinated species both increased pollen production and adaptations to increase pollen carry-over would increase the chance of pollen dispersal to more distant mates. Then pure males should be at an advantage over pollen-producing bisexuals, because males are without the heavy expenses of seed production, and should therefore have more resources available to divert to counteracting the potentially decreased pollination probability inherent in the physical nature of dioecism. Thus, an inherent consequence of dioecy, reduced number of potential mates, is increasingly negative as frequency of unisexuals increase; however, natural counteradaptations are possible which facilitate unisexuality.

The fact that only half the members of the dioecious population produce seeds also affects seed dispersal, and consequently, a seedling's chance of survival. In a dioecious population, seeds will be less uniformly distributed in space than for populations havng any other breeding system in which all individuals produce seed (given equal average dispersal distance, equal density of adults). The difference will be important, however, only in species with short-distance dispersal relative to the spacing of adults, where overlap of neighboring plants' seed dispersal "shadows" helps to make seed distribution more uniform. All else equal, less overlap of shadows of dioecious plants will occur because of greater distance between seed-producers. Consequently, there should be a less uniform post-dispersal seed distribution. This in turn could mean a lower risk of losing all of one's progeny through post-dispersal seed predation if seed predation rate was sensitive to distance between seed sources (Janzen, 1971; Bawa, 1980 independently arrived at this point also), or local seed density. However, if females had larger seed crops than hermaphrodites, as some expect (see above), then seed predation by a density-responsive predator ought to be greater for a dioecious population than for a bisexual one. Once dioecy is fixed in a population, the reduced seed predation could be an advantage which would tend to maintain dioecy. It would probably not influence the original evolution of dioecism, however, since the presence of bisexuals surrounding the dioecious plants would tend to keep seeds more evenly distributed. Again, this is a consequence of dioecism dependent upon frequency of dioecious plants within a population.

The most obvious consequence of reduction in the number of seed-bearers in a population, given that females do not produce more seeds than bisexuals, is a reduction in overall fecundity, or "r", the average per capita reproductive rate of a population (Lewis, 1942; Baker, 1959; Mulcahy, 1967; Heslop-Harrison, 1972; Freeman et al., 1980). In order to maintain the same average rate of parenthood as bisexuals, the females would have to produce twice the number of seeds as do bisexuals (Lewis, 1941), (and obviously, males would have to fertilize twice as many ovules as do bisexuals). Although some compensation in increased seed production is not uncommon (Ross, 1977), complete compensation seems unlikely. Theoretically, in an outcrossing hermaphrodite, resurces invested in male and female function should be equal (Charnov, et al., 1976; but see Horovitz, 1978). However, some empirical evidence indicates that this is not strictly true in practice (Primack and Lloyd, 1980; see also Chapter 2). In partially selfing bisexuals, where dioecy is likely to arise, there is evidence that investment in male and female functions are not equal (Smith and Evenson, 1978; Lemen, 1980; Primack and Lloyd, 1980; Freeman et al., 1980). Hence, although resources spent on male function in a bisexual may be shunted into seed production in a female, they may not be great enough to allow doubling of seed set. It should be pointed out that reduced fecundity does not necessarily preclude a net reduction in "r". As long as dioecy offers other advantages it may still increase the number of successful progency left by bearers of the trait.

Partial compensation by an increase in number of seeds may itself be an advantage under certain conditions. In particular, it has been argued that larger seed crops may allow satiation of seed predators or herbivores, and therefore a higher escape rate of seeds to seedlings (Bawa and Opler, 1975 after Janzen, 1971). However, larger seed crops might simply serve to attract predators or herbivores, thus having a negative effect. Similarly, it has been argued that wind-pollinated animal-dispersed species may gain by a greater attractiveness of large, concentrated seed crops (Givinish, 1980). Both Bawa and Opler and Givinish were prompted to these conclusions by finding a high incidence of dioecism among the type of species they describe. Unfortunately, the assumption that these species have larger seed crops than their bisexual ancestors has not been examined. Pertinent data are lacking and would be a valuable object of collection for future workers. It is known, that in some gynodioecious species females produce a greater biomass of seeds than do hermaphrodites (Darwin, 1877).

CONCLUSIONS

A summary of the consequences of dioecy that have been discussed ("Consequences of Dioecy"), as well as disadvantages ("Negative Effect") or advantages ("Positive Effect") arising because of each consequence is presented in Table 1-2. The table indicates which of these affect individuals carrying the dioecious trait immediately (I), vs. those that do not take effect until other members of the population

Table 1-2: Summary of negative and positive consequences of dioecy.

Aspects of Life Histories Affected by Dioecy	Negative Effect	Effect Immediate (I) or Frequency Dependent (F)	Co-adaptations which Reduce Negative Effect	Positive Effect	Effect Immediate (I) or Frequency Dependent (F)	Co-adaptations which Enhance Positive Effect
Sexual Specialization	Males may outcompete or overrun females because males spend less on sexual reproduction	I	None apparent	Resources available to females during seed ripening increases when phenology of sexes differs.	F	Males which become physiologically inactive (in annuals, senescent) after flowering.
				Ranges of available habitat increases when habitat utilization of males and females differs.	I	Long distance pollen dispersal
Outcrossing	Selfing not possible	I	For colonizing species: see below, Colonization.	Prevents selfing, reduces inbreeding depression	I	Previous outcrossing system undergoing a breakdown; most likely systems are coevolved pollinator, or dichogamy or temporal dioecy.
Pollination	Reduction in proportion of interplant moves (by pollen) potentially "correct" for pollination	F	Increase pollen production per male For insect pollinated species with many flowers per plant: decrease number of flowers open at one time per plant or separate time of day that male and female flowers open. For wind pollinated species: separate spatially male and female plants.	---	---	---

Table 1-2, continued.

Aspects of Life Histories Affected by Dioecy	Negative Effect	Effect Immediate (I) or Frequency Dependent (F)	Co-adaptations which Reduce Negative Effect	Positive Effect	Effect Immediate (I) or Frequency Dependent (F)	Co-adaptations which Enhance Positive Effect
Colonization	Decrease in colonizing ability because effective propagule is one male plus one female	I	Disperse seeds in clumps. For species with a series of transitory adult populations on one site: long term seed dormancy. Asexual reproduction.	---		
Physical Distribution of Pollen and Seeds	For males: reduction in number of potential mates within pollen distribution range	F	Increase pollen production per male. For wind pollinated spp.: more bouyant pollen. For animal pollinated species: increase pollen carry-over (e.g. stickier).	Seed predation may decrease because of increased heterogeneity in seed dispersion in the population.	F	None apparent
	Depression in "r" of offspring	I	Increase seed production per female.	Predation may decline due to satiation effects, or seed dispersal may improve, due to increased attractiveness of larger seed crops.		

are also dioecious, i.e., traits dependent upon frequency of unisexuals (F). Only "I" effects, those which have an immediate effect on an individual's fitness, can influence the initial spread of dioecy in a population. Effects labeled F may influence whether or not dioecy actually goes to fixation, and/or maintenance of dioecy in a population. Adaptations which minimize negative effects or enhance positive effects are indicated in columns labelled "Co-adaptations which Reduce Negative Effect", and "Co-adaptations which Enhance Positive Effect", respectively. Complimentary sets of traits which counteract negative consequences of dioecy and enhance the positive consequences may be seen by comparing these columns.

Whatever the initial selective pressures initiating the evolution of dioecy may be (whether related to genetic variation, inbreeding depression, higher seed output per plant), some of the innate consequences of dioecy make it unlikely to evolve in combination with just any life history strategy. Certain combinations of life history traits complement, or are complemented by dioecy, and are thus expected to be the most common sets found in nature. At this point, two patterns emerge.

1) Wind pollinated species (with capability for long-distance pollination) may reduce negative pollination consequences of dioecy and actually benefit by spatial segregation of the sexes. Spatial segregation of sexes may improve the pollination efficiency by allowing males and females to occupy particular sites best suited to their respective reproductive roles (dispersing/receiving pollen), something not possible with truly bisexual breeding systems. The total range of avilable habitat can increase when males and females segregate by

microhabitat utilization because males can occupy more marginal areas than seed-producing females or bisexuals. This promotes the maintenance of dioecism once it has evolved. Further, a mutation resulting in expression of only one sex, which sex depending upon environmental conditions, could be advantageous to a wind-pollinated species, particularly in marginal habitats. An individual possessing this trait could then be the sex best suited for reproducing in the site it landed in, and such a mutation might be favored.

2) Among insect-pollinated species, a "non-colonizing" life history may be another set of traits complementary to dioecy for species with many flowers per individual. For long-lived species such as trees and extensive cloners, the negative consequences of dioecy to colonization has little net effect on individual fitness because holding a site is more important to the number of offspring produced than is colonization. Some of the negative effect of dioecy on pollination effectiveness probably can be countered by a separation of time of day of floral activity in the two sexes. Other positive aspects of dioecism particularly enhanced for long-lived, insect-pollinated trees or cloners are prevention of clogging of stigmas with self pollen, and promotion of genetic variation among offspring. It is likely that in these types of species dioecy might originally arise in response to a breakdown in the out-crossing system. Prevention of inbreeding depression might be the initial advantage of dioecy, and other life-history traits could then facilitate fixation and maintenance of the trait.

To date only a very few comprehensive studies of the life history traits of specific dioecious species have been conducted. Many such studies will be needed before we can understand the consequences of dioecism, and hence, the evolution of this breeding system in plants. The following three chapters report results of an intensive study of the life history and population dynamics of a dioecious, perennial herb, *Valeriana edulis* Nutt. This study focuses on ecological consequences of sexual divergence.

CHAPTER 2

A COMPARISON OF LIFE HISTORY CHARACTERISTICS IN MALES AND FEMALES OF THE DIOECIOUS PLANT, *VALERIANA EDULIS* NUTT.

INTRODUCTION

Male and female reproductive strategies often differ in characteristic ways which are attributed to the basic polymorphism in male and female gametes. Males, having the smaller gametes, and presumably smaller production costs per gamete, but little physiological and quality control on offspring, would tend to have strategies emphasizing quantity of fertilizations accomplished (Williams, 1975). Females having fewer, but more expensive gametes, are more limited in the quantity of offspring they can produce; hence female strategies would tend to stress quality control of offspring (Williams, 1975). Given these conditions males would best increase their reproductive success by maximizing the number of eggs fertilized, often by obtaining multiple mates, and females would best increase their reproductive success by providing for the best growing conditions for their offspring (Bateman, 1949; Trivers, 1972; Williams, 1975). Such differences may lead to different ecology or behavior of the sexes, i.e., secondary sexual divergence.

In theory, for plants the relationship between expenditure on gametes and return in fitness differs between the sexes. Lloyd and Webb (1977) describe the expected situation pictured in Figure 2-1. A female's return should increase in proportion to investment until some physiological limit for reproductive expenditure is reached. Beyond this limit return would decline because of some drastic cost, e.g. decreased vigor. Potential male return/investment should increase more rapidly than female since so many more pollen grains than ovules can be produced per unit of investment. As saturation of ovules (within dispersal range of the male's pollen) is approached, the rate of return/investment declines, eventually reaching a level above which it can rise no further (a level set by ovule availability). Thus, the male curve reaches a plateau. Presumably, because each pollen grain is much smaller than a single ovule, a male can produce enough pollen to saturate available ovules at a lower level of total expenditure than the female's physiological limit. Hence, using an optimality argument, the maximum level of expenditure for a male of an iteroparous species is expected to be lower than that for a female (see Fig. 2-1).

Beyond the point where male return begins to plateau, male fitness should increase faster by investment of resources in growth or maintenance than by further investment in pollen production. If true, this would create a situation where the resource allocation scheme of males differs from that of females. Lower reproductive allocation by males allows males to have higher allocation to growth and maintenance than females (see discussions of resource allocation in Cody, 1966; Harper and Ogden, 1970; Gadgil and Solbrig, 1972). This difference in turn, could have some additional consequences, such as males having higher growth rates, and/or higher survivorship, and/or a greater number of reproductive cycles over their life span, than females. Lloyd and Webb (1977), reviewing sexual dimorphisim in dioecious plants hypothesized that many secondary differences between the sexes (e.g.,

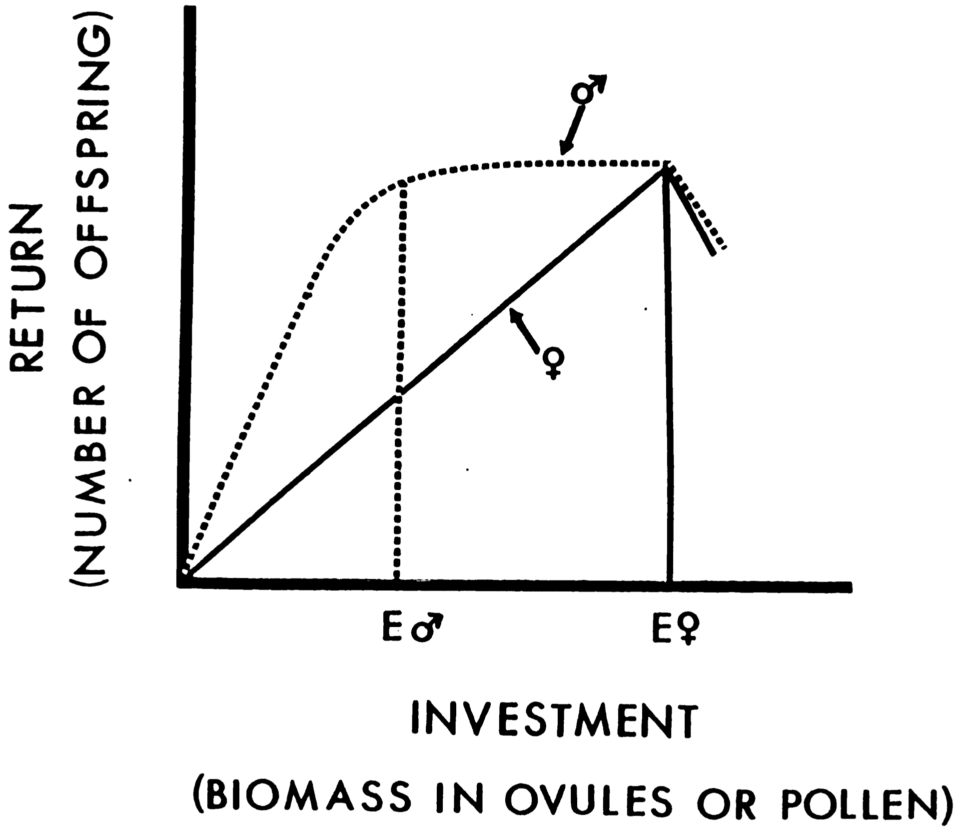

Figure 2-1: Theoretical relationship between the level of investment in gametes and the return in fitness for males and females. E♂ = expected maximum male investment; E♀ = expected maximum female investment.

greater vegetative growth and survival of males, niche utilization) were based upon differences in resource allocation.

Few actual measurements of male and female reproductive effort in dioecious plants have appeared in the literature to date. In *Rumex acetosella* male reproductive effort is lower than female and males have greater vegetative propagation (Putwain and Harper, 1972). In *Fragaria chiloensis* female reproductive effort is greater, but vegetative propagation is equal in males and females (Hancock and Bringhust, 1980). In *Simmondsia chinensis* female reproductive effort exceeds that of males if seed set is greater than 30% (Wallace and Rundel, 1979). Similarly, in *Silene alba*, when fruit set is greater than 20%, female reproductive effort is greater than male, but male exceeds female at lower percentages of fruit set (Gross and Soule, 1981). In this last study no growth differential was observed between the sexes, but other studies have reported females larger than males (ref's in Lloyd and Webb, 1977).

It is also possible that males and females could differ in age of sexual maturity. When males have lower resource allocation to reproduction than females, males should require lower minimum resource levels to support reproduction. Therefore males could develop a lower age of first reproduction than females (under selection for early reproduction). In many plants this would appear as males reproducing at smaller sizes than females.

It should be apparent from this brief discussion and review of the literature that males and females may differ in a number of life history traits: resource allocation patterns, age of maturity, longevity, and growth rates. In any particular species, which of these traits differ and how great are the differences between the sexes, ought to be connected to the other life history traits of the species. This expectation is based in the life history theory, which has predicted that certain suites of traits should be found together in species subjected to particular selective regimes.

Thus, studies of life history differences between the sexes in dioecious species are expected to reveal characteristic sets of divergent traits. Eventually, such studies can provide insight beyond the realm of the ecological consequences and evolution of the dioecious breeding system, by expanding understanding of how life history traits are interconnected. The special value of dioecious species in the latter context, is that there are two genetically distinct forms within the same species (males and females), which have different sets of constraints on reproductive success. This offers the opportunity of exploring the various responses to selection (comparisons of sexual divergence) under different selective regimes (comparisons of different populations) and within different constraining sets of life history traits (comparisons of different types of species).

An overview of the extent and significance of differences between the sexes in dioecious plants, will require data on reproductive effort and life history traits of males and females in species covering a variety of life histories. To date only four species have been investigated in this manner; two of these are cloning herbs (*Rumex acetosella* and *Fragaria chiloensis*), one is an annual, biennial, or short-lived perennial weed (*Silene alba*), and one is a desert shrub (*Simmondsia chinensis*). One life history conspicuously missing from this list is a non-cloning, perennial, iteroparous herbaceous species.

Although one such species, Chamaelirium luteum, an Eastern woodland species, was recently the subject of extensive study (Meagher and Antonovics, 1981) in which several forms of sexual divergence were found, no comparison of reproductive effort in males and females was made. Here, I present the results of a comparison of reproductive effort and other life history traits of the males and females in a dioecious perennial herb, Valeriana edulis Nutt., a species which grows in open meadows in the Rocky Mountain regions. I first document whether male reproductive effort is lower than female for this species. If support for this hypothesis is found in Valeriana edulis, then at least one of the following consequences should be seen: 1) males grow faster than females; 2) males survive longer than females; 3) males become reproductively mature earlier than females; 4) males flower more times in a lifetime than females.

DESCRIPTION OF PLANT, FIELD SITES, AND METHODS

The Plant

Valeriana edulis Nutt. is a long-lived, dioecious, insect-pollinated herb native to western North America. An abbreviated version of the description in the most recent monograph on the genus in North America (Meyer, 1951) follows. "Perennials 1'12 dm. tall, robust, from conical, often forked tap-roots...; multicipital caudex covered by numerous...leaf bases of previous seasons. Stem subscapose, 2-10 mm. thick...Leaves predominantly basal, imbricate, sometimes forming a rather loose rosette, linear or oblong- to obovate-spatulate, undivided or pinnate... (6-) 10-40 cm. long, .3- 4.2 (-6.5) cm. wide, gradually tapering to the subpetiolar base...' cauline leaves 2-6 pairs, pinnate to pinnatifid, rarely undivided, short-petiolate or sessile below, much reduced and bract-like above, 3-22 cm. long... Inflorescence 10-45 (-75) cm. long, 2-14 cm. wide in anthesis, later diffuse, 14-65 cm. long, 2.5-17.0 cm wide... Corolla rotate, that of the pistillate flower minute, about 0.5 mm. long, of the staminate flower 2.5-3.5 mm. long, white, glabrous or pilosulous towards the base of the tube without, the lobes half as long as to equaling the straight tube... Achenes 2.5-4.5 mm. long,... broadly ovate to ovate-oblong or oval,... 1.5-3.0 mm. wide..." (See Figure 2-2).

"DISTRIBUTION: In moist pastures, creek bottoms, yellow pine and aspen woods, sagebrush plains, limestone cliffs, and subalpine parks, 5500-11000 ft. alt., southern British Columbia, western United States (except California) to northwestern Mexico. Flowering and fruiting May to September" (Meyer, 1951). The flowers are pollinated by various insects, including some flies and moths (personal observation).

V. edulis has been described as dioecious by Barrell (1969) and polygamodioecious by Meyer (1951). This discrepancy may be partially due to the fact that there are three distinct subspecies. In the region of this study the species is *V. edulis* ssp. *edulis*, (Meyer, 1951; Barrell, 1969) and plants are dioecious, with very low frequencies of male plants which produce a few seeds.

The study was undertaken in Gunnison County, Colorado, at the Rocky Mountain Biological Laboratory, near Crested Butte. Populations were all in subalpine parks, between 8800 and 11500 feet elevation. Apparently this is excellent habitat for this species, since plant measurements were larger here than in the description given above (here up to 14 dm tall, root crown up to 45 cm diameter with tap root as much

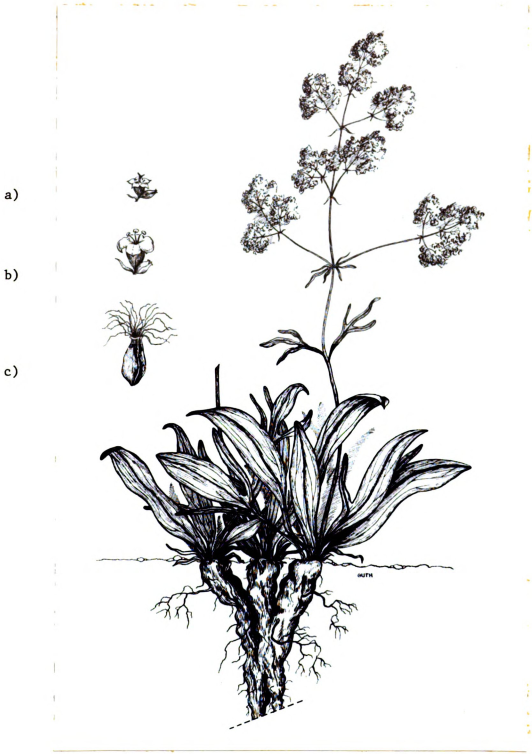

Figure 2-2: Growth form of *Valeriana edulis* Nutt. Actual size is 1m tall; a) female flower, 1.5mm diameter; b) male flower, 2.5mm diameter; c) mature fruit, 3.5 mm length.

as 10 cm diameter at the top, 1 to 20 stems per flowering plant). The tap root cannot be aged directly because of distortion of tissues caused by the action of contractile roots which obscures growth rings. Nevertheless, ages can be estimated from growth rates of individuals; growth rate data for plants in this region indicate that the largest plants are 20 to 300 years old, while the average-sized individuals range from seven to 23 years old, depending on the population sampled.

Field Sites

Four populations were studied in detail (named BCP, BCR, NRG and BI) (see Chapter 3 for a description of the sites). Six other populations were examined in less detail. Values for characters obtained from the four main populations are comparable to averages obtained from all 10 populations, and show that the four main populations are representative of the species as a whole in the region of study (Table 2-1).

Survival and Monitoring

In 1978, in each of the four main populations, 150 plants were chosen by random point selection, and marked with metal tags (600 total). These included 50 males, 50 females, and 50 plants not flowering in that season (termed vegetative, subsequently) per population. In 1979 additional plants were marked within square grids in three of the populations (one population was too heavily grazed by cattle to maintain a grid). In each grid, all plants of *V. edulis* were marked. These two sets of plants will be referred to as random-marked and grid-marked plants, respectively. Random-marked plants were censused again in 1979 and 1980 and grid-marked in 1980. Many random-

Table 2-1. Plant characteristics calculated from samples from 10 vs. 4 populations of *Valeriana edulis* .

	Sample Size	
Characteristic	10 populations	4 populations
number of inflorescences/plant	2.56	2.55
Plant diameter	10.78 cm	9.51 cm
density of flowering plants	0.42 plants/m^2	0.74 plants/m^2
sex ratio	35.82% males	36.18% males

marked plants (about 25%) were not found in 1979 due to tag loss, so maps were prepared at this time, and in 1980 nearly all plants were found. Table 2-2 shows the sample sizes for each population, in each season.

Survival data were obtained directly for all tagged plants in which tags were recovered in succeeding seasons. Survival over three seasons is known for 398 of the plants random-marked in 1978. Survival over two seasons is known for 364 of the plants grid-marked in 1979.

In addition, some inferences about relative survival rates in males and females can be made from knowledge of the size structure of males compared to that of females and their respective growth rates. Here size refers to basal diameter (see below). Size structure of males and females was compared with the Kolamogorov-Smirnov goodness of fit test (Sokal and Rohlf, 1969).

Reproductive Effort

Reproductive effort has been defined as the proportion of an individual's resources devoted to reproduction (Harper and Ogden, 1970; Gadgil and Solbrig, 1972: Abrahamson and Gadgil, 1973). This has usually been approximated in plants by the proportion of total biomass, or annual biomass, devoted to reproductive structures (e.g., Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Gaines et al., 1974; Hickman, 1975; Werner and Rioux, 1977; Holler and Abrahamson, 1977; Soule and Werner, 1981). Although this measure is only a crude estimate of the proportion of resources devoted to the reproductive function, biomass allocation patterns have proven in several cases to reliably reflect the caloric allocation pattern (Abrahamson and Gadgil,

Table 2-2. Tag recovery and sampling regime in 4 study populations.

	Populations				
NUMBER OF:	1-BCR	2-BCP	3-NRG	4-BI	TOTAL
1. plants random-marked in 1978	150	150	150	150	600
a. tagged plants refound in 1979	109	96	112	131	448
b. tagged plants refound in 1980	103	71	110	128	412
2. plants grid-marked in 1979	123	----	148	94	365
a. tagged plants refound in 1980	123	----	147	94	364

1973; Hickman and Pitelka, 1975; Snell and Burch, 1975; Wallace and Rundel, 1979; but see Jolls, 1980 for a contradictory case); nutrient allocation patterns have usually been too complex to provide enlightenment on resource allocation (Caswell and Welton, 1979; Van Andel and Vera, 1977), but in one study, proportional allocation of nitrogen, phosphorous and glucose-equivalents was similar to the allocation of biomass and calories (Wallace and Rundel, 1979).

Most studies calculating reproductive effort reported are concerned with short-lived plants. Here I am dealing with a large, long-lived plant. Because of the large size of many plants, and the heavy impact of removing them from public, relatively undisturbed lands, I sought a non-destructive method of obtaining comparable biomass allocation data. Correlations between stem weight and stem height, and leaf weight and number of basal leaves or leaf bundles were obtained from 20 plants destructively sampled. The correlation of leaf dry weight vs. number of leaf bundles was highly significant with $r = 0.955$. Height of male and female inflorescences were significantly correlated with inflorescence dry weight (male $4 = 0.581$, $p < 0.01$; female $r = 0.644$, $p < 0.01$). Components of the regression equations are given in Table 2-3. Inflorescences were designated as the entire inflorescence stem because these stems are nearly leafless, only produced by flowering individuals, and primarily function to support flowers (see Figure 2-2). Then, I measured inflorescence height and number of leaf bundles for 39 living males (19 in 1979 and 20 in 1980) and 51 living females (30 in 1979 and 21 in 1980) and used the regressions to calculate the percentage of above-ground weight (annual biomass) in reproductive parts, i.e., reporductive effort.

Table 2-3. Components of linear regressions for leaf bundle number and inflorescence height vs. dry weight

Dry Weight vs.:	slope	y-intercept
Number of leaf bundles	1.64	-0.77
Male inflorescence height	0.0849	-3.44
female inflorescence height	0.049	-0.66

Root weight was not included for two reasons: (1) the aboveground parts are entirely annual tissue whereas there is a large, unknown proportion of perennial tissue in roots; and (2) the extreme disturbance caused by removing roots. The plants used to calculate reproductive effort came from two of the four populations. One population (the hightest site, BI) was omitted because plants did not achieve fully elongated stems (the condition used in obtaining the original regressions) during the period of study due to late initiation of flowering at high altitudes. The other (BCP) was omitted because data on mature plants were not obtained due to extreme disturbance by cattle pastured in this area just prior to the appropriate sampling time.

Seed weight was later added to the female reproductive effort calculated above, because samples for inflorescence weight-height regressions were taken at anthesis, prior to seed set. Therefore female reproductive effort is estimated 2 ways: first including flowers only, and second including seed production. The latter is thus slightly overestimated because ovule tissue is essentially weighed twice. Results of reproductive effort calculations were analyzed using 2-way ANOVA's for effects of sex and plant size on reproductive effort. One analysis compared males and females at anthesis, another compared males at anthesis to females at seed set. The method of determining size classes for these analyses is explained below.

Growth Rates

The annual growth rate was obtained directly by measuring marked individuals in successive seasons. Crown diameter, measured at the base of leaves, is a measure of the amount of perennial tissue accumulated in a plant, since these plants grow by lateral budding at the periphery of the crown. This is not a mode of vegetative propagation since no fragmentation occurs and plants have a single tap root. Average annual change in size of perennial tissues represents the net gain or loss of biomass after all reproductive and maintenance costs are incurred. Crown diameter was measured in July (BCP, BCR) or August (NRG, BI) of 1978, 1979, and 1980 for random-marked plants, and in the same months in '79 and '80 for grid-marked plants. In addition, leaves or leaf bundles were counted for all plants in '79 and '80. (A "leaf bundle" is a discrete, tight rosette of leaves; see Figure 2-2; for plants with fewer than five leaf bundles, individual leaves were counted; for all plants, the number of leaf bundles was counted.) Plants were classified into size classes of 1-4, 5-8, 9-10, 11-17, or 18-38+ cm diameter, chosen by Vandermeer's method of size class estimation for use in a stage projection matrix population dynamics model (Vandermeer, 1978). This method selects size categories so as to minimize the error due to both sampling and distributions. Because growth rates may vary with age or size, classifying plants by size allows a more refined comparison of growth rates (and other measurements) for each sex. These same size categories are used throughout this study in other analyses.

Analysis of preliminary growth data in 1979 by ANOVA for paired comparisons (Sokal and Rohlf, 1969) revealed that significant growth occurred between 1978 and 1979. Thus, sample sizes were large enough to detect significant growth despite high variance in growth rates. To analyze the effects of sex and plant size on growth rate, a two-way

ANOVA with an adjustment for unequal sample size (Snedecor and Cochran, 1967) was employed. A preliminary test showed that the data from the two seasons (1978-1979, and 1979-1980) should not be pooled due to heterogeneous variance. Therefore, the two seasons were analyzed separately. Plants were placed in size classes according to their size at the start of the growth period (i.e., size in 1978 for the 1978-1979 growth, and size in 1979 for the 1979-80 growth). A third analysis, the average annual growth from 1978 to 1980 for plants measured all three seasons, was also carried out.

The average growth of males and females was calculated from the size-specific rates weighted by the size structure of each sex in the four populations combined. The size structure was obtained from random samples taken for the purpose of determining density in each population.

Effect of Flowering on Growth Rate

To determine whether an immediate effect of flowering on growth rate could be detected, plants were classified by flowering history: plants which flowered one season, but did not flower (were vegetative) the following season (flowering year growth rate, Table 2-4); and plants vegetative in one season, and flowering in the following season (pre-flowering year growth rate, Table 2-4). Flowering and preflowering growth rates were then compared for males and females using a two-way ANOVA. The 1978-1979 season was analyzed separately from the 1979-1980 season because variance in growth rates was heterogeneous between the two seasons, and because for the 1979-1980, a "control" set of plants was available and also included. The "control"

Table 2-4. Classification of plants by flowering history for analysis of effects of flowering history on growth rates in <u>Valeriana edulis</u>; Asterisks indicate state of a plant in the given year, FL = flowering, or VEG = vegetative.

		Flowering History					
		1978		1979		1980	
Growth Category		FL	VEG	FL	VEG	FL	VEG
Flowering year	a)	*			*		
	b)			*			*
Preflowering year	a)		*	*			
	b)				*	*	
Adult vegetative		*			*		*

was adult vegetative growth, obtained from plants which were vegetative in both 1979 and 1980, but had previously flowered in 1978 (Table 2-4).

In a second approach I analyzed the effect of number of flowering episodes on growth rate over three years, 1978-1980. Plants were classified by the number of times they flowered, once, twice or three times, during the three seasons (regardless of which years flowering occurred), and their growth rates analyzed by ANOVA.

Onset of Reproductive Maturity

Remnants of old flowering stems are visible on plants which flowered in the previous year, and presence or absence of these old stems constituted evidence for previous flowering. Average size at onset of reproductive maturity was estimated for each sex by categorizing plants by size and known flowering history and determining the size below which 90% of all flowering plants had no record of previous flowering. The 90% criterion was an arbitrary choice, so to check on the influence of this choice, a second criterion, 50% was also used. Because it appeared that the smallest size class determined by Vandermeer's method (see above) contained the critical sizes, this class was broken down into the smallest categories possible (1 cm. intervals). The size below which 90% or more of the flowering plants had no record of previous flowering was considered the best estimate of average size at first flowering for purposes of comparing males and females. It is not meant to be a precise estimate of the size of reproductive maturity.

Flowering Frequency and Reproductive Effort per Year

Flowering frequency was determined for random-marked plants during three growing seasons, simply by repeated censusing. These data are presented as the average number of times plants flowered per year for each size class of plants.

Results were analyzed by a two-way ANOVA for size and sex effects on flowering frequency. An _a posteriori_ Student-Newman-Keuls test (SNK test; Sokal and Rohlf, 1969) was used to test differences among size class means.

Average reproductive effort per year for each size class and sex was calculated by multiplying the reproductive effort for plants in flower by the probability of flowering (flowering frequency).

RESULTS

Reproductive Effort

Comparing males and females at anthesis, females had a higher allocation to reproduction than males in the two smallest classes, but similar allocations in the two larger classes (Table 2-5). At anthesis no significant difference between the sexes occurred ($F_{sex} = 2.01$; $F_{(1,81)} = 3.96$). However, total female reproductive effort including seed set was 4% to 7% higher than at anthesis (Table 2-5), and the corresponding ANOVA comparing total reproductive effort for females to total for males revealed a significant effect due to sex. Thus, the prediction that male reproductive effort would be lower than female held true.

In both sexes, reproductive allocation was highest in the smallest plants, and both ANOVAs showed significant variation among the different sized plants. Testing which size classes differed from one another, an _a posteriori_ SNK test (Sokal and Rohlf, 1969) revealed that

Table 2-5. Reproductive effort (% above-ground biomass in inflorescences) in *Valeriana edulis* for four[1] size classes.

	% of above ground biomass in inflorescences $\bar{x}$ ± SE		
	MALES	FEMALES	
Size Class	Total (at anthesis)[2,3]	At Anthesis	Total (including seeds)[3]
1-4 cm[4]	58.21 ± 4.12	67.25 ± 2.33	73.23
5-8	39.53 ± 4.49	45.75 ± 4.27	52.59
9-17[1]	39.15 ± 3.80	38.54 ± 5.50	43.71
18-38	38.99 ± 4.93	41.26 ± 3.98	48.61

---

[1] Two categories were lumped here because of insufficient data for the category 9-10 cm

[2] Differences among the size classes significant by ANOVA (F = 17.10, d.f. = 3, 81, $p << 0.01$). Analyses used arsin /p transformation.

[3] Differences among the size classes and between the sexes significant by ANOVA; Size (F = 16.51, d.f. - 3, 81, $p << 0.01$), Sex (F = 13.47, d.f. = 1, 81, $p << 0.01$).

[4] The mean reproductive effort in this size class was significantly different from that in all other size classes by Student-newman-Keuls test; $p < 0.05$.

the only significant differences were between the smallest class and each other class.

Because *V. edulis* females alone bear the costs of seed maturation and ultimately spend more on each reproductive episode than males, I expected to see some costs of higher reproductive expenses in females. As predicted earlier, these should appear as differences between the sexes in other aspects of life history, in particular, in flowering frequency, size at maturity, growth or survival.

Flowering Frequency and Reproductive Effort per Year

The average flowering frequency was lower for females than for males, both overall and in every size class (Table 2-6) as predicted earlier. Significant effects of both size and sex on flowering frequency were found in the ANOVA. In fact, means of all size classes were significantly different from one another except for the plants 9-10 cm compared to plants 11-17 cm (Table 2-6).

The average reproductive effort per year of females in each size class was higher than that of males, but the difference between the sexes here was much less dramatic than when reproductive effort per flowering episode (RE of flowering plants only) was compared (Table 2-7). Apparently higher male flowering frequency does not totally compensate for lower male reproductive effort. The annual reproductive effort was fairly uniform across size classes for all but the largest size category which had the highest reproductive allocation in both sexes.

Onset of Reproductive Maturity

The estimated size at first flowering (size below which 90% or

Table 2-6. Flowering frequency in Valeriana edulis classified by sex[1] and plant size[2].

	Number of Flowering Episodes in 3 years x ± SE, n = sampling size				Flowering frequency per year.	
Plant Diameter	n	Males	n	Females	Males	Females
1-4cm	29	1.48 ± 0.14	40	1.35 ± 0.08	0.49	0.45
5-8	48	2.06 ± 0.11	54	1.85 ± 0.10	0.69	0.62
9-10[3]	25	2.36 ± 0.14	18	2.28 ± 0.18	0.79	0.76
11-17[3]	30	2.57 ± 0.10	49	2.39 ± 0.10	0.86	0.80
18-38	22	2.91 ± 0.06	21	2.81 ± 0.09	0.97	0.94

[1] Effect of sex significant by ANOVA, $p<0.05$ ($F_{(1,\ 326)} = 4.572$).

[2] Effect of size significant by ANOVA, $p<0.01$ ($F_{(4,\ 326)} = 40.720$); effect of size x sex interaction not significant.

[3] means in these two size classes not significantly different by SNK tests; all other differences between size class means were significant

Table 2-7. Annual reproductive effort in Valeriana edulis classified by plant size, a) males, reproductive effort at anthesis; b) females, reproductive effort including seed set. Average reproductive effort per year = RE/flowering episode x probability of flowering per year.

	Plant Size	Total Reproductive Effort/ Flowering episode	Flowering Probability	Average Reproductive Effort per year
a) males	1-4cm	58.21%	0.49	28.77%/yr
	5-8	39.53	0.69	27.18
	9-10	39.15	0.79	30.80
	11-17	39.15	0.86	33.50
	18-38	38.99	0.97	37.81
b) females	1-4cm	73.23	0.45	32.95%/yr
	5-8	52.59	0.62	32.46
	9-10	43.71	0.76	33.18
	11-17	43.71	0.80	34.79
	18-38	48.61	0.94	45.52

more of the flowering plants showed no evidence of previous flowering) was smaller for males than females, again, as predicted earlier. For males, 90% of all plants flowering between the sizes of 1 and 2 cm had no evidence of previous flowering. This gives an estimated size at first flowering for males of 2 cm or less (Table 2-8). For females this estimated size at maturity was 4 cm or less. The 50% criterion (see methods) gives estimates of 8-10 cm for males, and 11-13 cm for females. Both the 50% and 90% criterion result in a smaller estimated size at first flowering for males than for females.

Growth Rates

The average annual growth increment for females in the first season (1978-1979) was lower than that for males (Table 2-9a). However no significant effect of sex appeared in the ANOVA of size specific growth rates from this season (Tables 2-9a and 2-10). In the second season (1979-1980) the situation was reversed, and the average female growth increment was greater than that of males (Table 2-9b). Further, the ANOVA for this year showed significant sex, size, and sex-size interaction effects (Tables 2-9b and 2-10). Among individuals followed through both seasons the average male growth rate was slightly higher than the female growth rate (Table 2-9c). Again, as in the first season, there was no significant effect of sex in the ANOVA (Tables 2-9c and 2-10). Thus, the relationship between the annual growth rates of males and females differs from year to year, and growth rates of males do not consistently differ from those of females in *Valeriana edulis*. The prediction made earlier, that male growth should exceed female does not hold true.

Table 2-8. Size at first flowering in *Valeriana edulis*: occurrence of plants with no evidence of previous flowering in each size class for males and females.

	Percent of flowering plants with no evidence of previous flowering			
Plant diameter	*n*	Males	*n*	Females
1 cm	22	95.45	29	100.00
* 2	12	83.33	17	94.12
3	22	72.73	22	95.45
** 4	23	47.83	39	79.49
5	26	69.23	44	70.45
6-7	31	58.06	53	49.06
† 8-10	45	31.11	67	56.72
‡ 11-13	35	25.71	38	39.47
14-18	29	27.59	51	27.45
19-38	36	13.89	60	13.33

* estimated size of first flowering for males, using 90% criterion (see text).

** estimated size of first flowering for females, using 90% criterion.

† estimated size of first flowering for males, using 50% criterion.

‡ estimated size of first flowering for females, using 50% criterion.

Table 2-9. Annual growth rate of males and females for standard size classes, and overall[†]; a) 1978 to 1979 season; b) 1979 to 1980; c) 1978 to 1980.

		Growth rate: change in diameter (cm/year) x ± SE and sample size (n)	
	Size Class	Males	Females
a)	1-4 cm	0.92 ± 0.41 (26)	0.50 ± 0.34 (40)
	5-8	1.02 ± 0.53 (52)	0.40 ± 0.36 (52)
	9-10	1.34 ± 0.66 (32)	-0.44 ± 0.78 (25)
	11-17	-0.44 ± 0.63 (36)	-0.57 ± 0.72 (54)
	18-38	-0.96 ± 1.16 (25)	-0.71 ± 1.58 (24)
	overall[†]	0.48	0.005
b)	1-4 cm	0.97 ± 0.26 (59)	0.87 ± 0.16 (99)
	5-8	0.55 ± 0.32 (67)	0.65 ± 0.29 (97)
	9-10	0.71 ± 0.86 (35)	0.02 ± 0.38 (40)
	11-17	-0.33 ± 0.44 (66)	0.13 ± 0.40 (76)
	18-38	-2.90 ± 0.81 (39)	-0.96 ± 0.55 (56)
	overall[†]	0.05	0.32
c)	1-4 cm	0.52 ± 0.16 (31)	0.78 ± 0.22 (43)
	5-8	0.47 ± 0.35 (48)	0.34 ± 0.17 (58)
	9-10	0.64 ± 0.33 (26)	0.28 ± 0.45 (20)
	11-17	0.08 ± 0.38 (31)	0.14 ± 0.36 (48)
	18-38	-0.48 ± 0.64 (21)	-0.65 ± 0.60 (24)
	overall[†]	0.30	0.16

[†] overall values are an average of the values for each size class weighted by the random size structure in the four study populations.

Table 2-10. Results of 2-way analysis of variance for effects of size and sex on growth rates.

	Significance level of:		
Period of Growth	Size Effect	Sex Effect	Size-Sex Interact
'78 to '79	n.s.	n.s.	n.s.
'79 to '80	**	**	*
'78 to '80	*	n.s.	n.s.

n.s. = not significant

* = $p<0.05$

** = $p<0.01$

In both sexes, and in both seasons, growth rates tended to decline as plant size increased, with the lowest rates falling in the largest size class and, in fact, consistently negative (Table 2-9). The effect of size was significant in the second season and across the two-year average (Table 2-9). However, in the second season sex and size interacted such that in the 1-4cm and 9-10cm size classes males had higher growth rates than females. In the other three size classes, female rates exceeded those of males. The biological significance of this particular interaction is not readily apparent.

In the largest size class, growth rates were negative in all analyses (Table 2-9). Dissecting the growth rates into shrinking, growing and static plants (Table 2-11) revealed that the largest size category had both the highest proportion of plants shrinking, and the highest shrinkage increment among shrinking plants. At the same time, the growth increments for plants which grew were greatest in the largest plants.

Effect of Flowering on Growth Rate

From 1978 to 1979, no significant difference was found between the growth of plants classified as flowering, and those classified as preflowering. Sex, and interaction effects were not significant either (Table 2-12). In the second season, 1979-1980, a significant effect of flowering history was found, such that flowering plants grew less than preflowering plants (Table 2-12). In this analysis the sexes did not differ significantly in growth, nor did the growth of plants flowering in either 1979 or 1980 (flowering + preflowering) differ from the growth of adults not flowering either year (Table 2-12). There is a

Table 2-11. Size-specific probability of growing, remaining the same size, or shrinking, and mean size change for growing and shrinking categories for a) males and b) females of *Valeriana edulis* during the period of 1978-1980.

a) MALES

	Probability of				Size change, cm, $\bar{x}$ ± SE	
Size	GROWING	STAYING SAME	SHRINKING	n	GROWING	SHRINKING
1-4cm	0.6774	0.1292	0.1935	31	0.98 ± 0.15	-0.75 ± 0.11
5-8	0.5600	0.1200	0.3200	50	1.50 ± 0.25	-1.03 ± 0.20
9-10	0.5769	0.1154	0.3077	26	1.59 ± 0.32	-1.29 ± 0.26
11-17	0.4194	0.1613	0.4194	31	1.81 ± 0.35	-1.78 ± 0.43
18-36	0.4286	0.0000	0.5714	21	2.22 ± 0.51	-2.50 ± 0.54
b)FEMALES						
1-4cm	0.6774	0.1163	0.2093	43	1.34 ± 0.26	-0.61 ± 0.07
5-8	0.4655	0.1379	0.3966	58	1.37 ± 0.21	-0.76 ± 0.08
9-10	0.4286	0.1429	0.4286	21	2.06 ± 0.44	-1.44 + 0.32
1-17	0.4792	0.1250	0.3958	48	1.98 ± 0.33	-2.05 ± 0.44
18-38	0.4167	0.8333	0.5000	24	2.10 ± 0.47	-3.04 ± 0.51

Table 2-12. Effect of flowering history on growth rate in *Valeriana edulis*, I. Flowering year vs. preflowering year growth in males and females.

	Growth, cm/yr, x ± SE, (sample size)	
1978-79 Growing season[1]	MALE	FEMALE
Flowering	-0.60 ± 0.51 (42)	-0.83 ± 0.55 (47)
Preflowering	0.81 ± 0.76 (21)	-0.39 ± 0.47 (46)
1979-1980 Growing Season[2]		
Flowering	-0.81 ± 0.61 (31)	-0.46 ± 0.60 (26)
Preflowering	0.82 ± 0.43 (33)	0.18 ± 0.44 (33)
Adult vegetative	-1.41 ± 0.92 (17)	-0.04 ± 0.52 (27)

[1] Effects of sex and flowering history not significant in ANOVA.

[2] Effect of flowering history significant, $p<0.05$ ($F_{(2, 161)} = 3.91$); Effect of sex not significant; Flowering growth significantly different from preflowering growth, $p<0.05$ ($F_{(1, 161)} = 4.65$); Flowering and Preflowering growth not significantly different from adult vegetative growth.

suggestion here that the trade-off between growth and reproductive expenses predicted earlier, sometimes holds in V. edulis.

In a second way of examining a potential trade-off between growth and reproduction I analyzed the effect of number of flowering episodes on growth rate. Since a preliminary analysis showed that in the data from 1978 to 1980 this effect was independent of sex, the sexes were pooled and the category of plants which did not flower at all during this period (sex unknown) was also included in the analysis. This ANOVA showed a significant effect of number of flowering episodes (Table 2-13); the more times plants flowered, the higher were their growth rates. The growth of triple-flowering plants was significantly greater than that of both single-flowering and non-flowering (juvenile) plants, using an a posteriori SNK test to test for differences between means. Rather than a trade-off between growth and reproductive expenses, these data indicate a positive relationship between expenditure in these categories.

Survival

Survival of 174 males and 211 females followed from 1978 to 1980 (random-marked plants) is shown in Table 2-14. Males survived at an annual rate of 96.0%, while females survived at a rate of 96.4% per year. Grid-marked males had a rate of 97.3% survival from 1979 to 1980, while the corresponding female rate was 98.9% (see Table 2-14). The male and female rates of survival were not significantly different when tested with a chi-square test. Once again, the earlier expectation of higher male than female survival was not upheld.

Size distributions of males and females are given in Table 2-15.

Table 2-13. Effect of flowering history on growth rate in *Valeriana edulis*, II. Cumulative effect of number of flowering episodes during three years of study.

Number of Flowering Episodes	Sample Size	Growth, cm/yr $\bar{x} \pm SE$
0	25	-1.20 ± 0.48^{a}
1	92	-0.23 ± 0.34^{a}
2	113	$0.27 \pm 0.35^{a,b}$
3	132	1.21 ± 0.38^{b}

^{a,b}indicate means not significantly different by Student-Newman-Keuls test (Sokal and Rohlf, 1969).

Table 2-14. Survivorship of males and females in *Valeriana edulis*.

RANDOM-MARKED PLANTS	Males	Females
Sample size (alive in 1978)	174	211
Plants dead in 1979	2	0
Plants dead in 1980	12	15
$\bar{x}$ number dying/year	7	7.5
% surviving/year	95.98	96.44
GRID-MARKED PLANTS		
Sample size (alive in 1979)	112	188
Plants dead in 1980	3	2
% surviving/year	97.32	98.94

Table 2-15. Comparison of size-structure of males and females of *Valeriana edulis* in random samples pooled from four populations.

	Cumulative Frequency		
Size class	males	females	Difference, male-female
1-5cm	0.3614	0.3506	0.0108
6-10	0.6554	0.6335	0.0219
11-15	0.8175	0.7850	0.0325$^{d\text{-}max}$
16-20	0.8918	0.9072	-0.0154
21-25	0.9661	0.9593	0.0068
26-30	0.9830	0.9864	-0.0034
31-35	0.9864	0.9954	-0.0090
36-40	0.9999	1.0000	-0.0001
number in sample	296	442	

$^{d\text{-}max}$is the Kolmogorov-Smirnov goodness of fit test statistic for comparison of male and female size distributions. This value is not significant ($d_{(0.05)} = 0.0466$).

No significant differences were found between the size distributions of the sexes using a Kolmogorov-Smirnov goodness of fit test. Survival rates of different sized plants were compared for males and females (Table 2-16). Survival appeared to be lowest in the smallest size class for males, but this was not true of females. Survival in females was lowest in the largest size class.

DISCUSSION

The predicted difference in reproductive effort between the sexes is upheld for *Valeriana edulis*; male reproductive effort per flowering episode is indeed lower than female. Several of the expected consequences of this initial difference also occur. Males flower more frequently than females, as predicted. Consequently, average male reproductive effort per year is closer to the female level than in the comparison of effort per flowering episode, but still consistently lower than female. Males also mature at smaller sizes than females, as predicted. However, no consistent differences between the sexes in growth rates was found, nor were any clear indications of the predicted trade-off relationship between growth and reproduction. Similarly, predicted higher male survival was not found; the average survival rates of males and females were not significantly different from one another.

Differences Between the Sexes in Reproductive Effort and Schedules

One aspect of the pattern of reproductive allocation in *Valeriana edulis* emerges as especially interesting: total reproductive allocation (including seeds) is greater for females than males, but when the sexes are compared at anthesis (no seeds included) male

Table 2-16. Survival in plants of different sizes (*V. edulis*).

	Survival rate (sample size)	
Size class	MALES	FEMALES
1-4 cm	0.88 (35)	0.93 (46)
5-8	0.94 (51)	0.97 (60)
9-10	0.93 (28)	1.00 (20)
11-17	0.91 (35)	0.89 (54)
18-38	0.91 (23)	0.86 (28)

reproductive allocation is nearly as great as female. Apparently it is the maturation of seeds by females that differentiates the expenditures of the sexes, rather than a differential in expenditure towards fertilization. A similar pattern of reproductive expenditure, with female investment exceeding male only with the inclusion of seed set, has been found in the two other studies which examined this point (dioecious species, Simmondsia chinensis, Wallace and Rundel, 1979; and Silene alba, Gross and Soule, 1981). In these cases male effort actually exceeded that of females prior to the seed maturation period of females. One explanation for equality of pre-fertilization expenses of the sexes is that costs of gamete production may be swamped by secondary costs of reproduction, i.e., costs of flowers, nectar, and support structures. Additionally, it may take a very large quantity of pollen to fertilize each ovule in these species, and therefore total costs of pollen and ovule production may be similar.

According to this explanation, only dioecious species with particular growth forms would be expected to exhibit equal costs of reproduction in males and females up to fertilization., i.e., those with large inflorescences, like V. edulis, and perhaps those with large, elaborate flowers or copious nectar production. The dioecious Umbelliferae in New Zealand have large inflorescences (Lloyd, 1973) and thus might be expected to also show equal investment by the sexes up until seed maturation. On the other hand, large, elaborate flowers are not common among dioecious species; most tropical trees studied so far have small, unspecialized flowers (Bawa and Opler, 1975), and most temperate species are wind pollinated (Baker, 1959; Freeman et al. 1980). Unfortunately, pertinent data on reproductive effort are not available.

In Valeriana edulis, males flower more frequently than females. This is also true in Chamaelirium luteum (Meagher and Antonovics, 1981) and in the five other species for which this data is available: Asparagus acutifolius, Trichilia monadelphia, Aciphylla aurea and A. subflabellata, and Aralia nudicaulis (reviewed in Lloyd and Webb, 1977). Although my data clearly indicated that for each reproductive episode males of V. edulis have a lower reproductive allocation than females, to get an accurate view of life-time effects on fitness it is necessary to consider the average allocation to reproduction per year. As long as the life span of females and males of V. edulis are equal, males must flower more times in a lifespan than do females, on the average because males flower more frequently. Nevertheless, the average reproductive effort per year of males is still lower than that of females, and consequently, the lifetime reproductive effort of males is lower. Although no direct data on lifespan of males and females were gathered, the fact that growth rates, survival rates and size distributions did not differ between the sexes is fairly strong evidence of equal longevity. The data on V. edulis points out that in a long-lived species, a considerable difference between the sexes in seasonal reproductive effort may be partially compensated by differing flowering frequency of the sexes, so that total lifetime reproductive effort, may be less dramatically different in males and females. Data on lifetime reproductive effort, or even reproductive effort per year have not been reported for other species, to my knowledge. Both of these factors are of basic importance in interpreting sexual differences in light of life history theory.

The fact that in *V. edulis* male effort is distributed across more flowering episodes, starting earlier in life (i.e., when smaller), may have important consequences to a male's fitness compared to a female's. Earlier reproduction essentially reduces the generation time of males relative to females, conceivably increasing a male's fitness. On the other hand, more frequent flowering by males should increase the proportion of functional males in the population (the expressed sex ratio) during any one flowering episode, with the consequence of reducing any one male's chance for paternity per flowering episode.

Valeriana edulis males reproduce at a smaller size than females. This was also found to be the case in *Chamaelirium luteum* (Meagher and Antonovics, 1981), *Ilex opaca* (Clark and Orton, 1967), and *Clematis gentianoides* (Godley, 1976). Melampy and Howe (1977) similarly found small sized males of *Triplaris americana* reproducing more frequently than females. It is of interest whether or not males incur any extra risk for early reproduction. Melampy and Howe (1977) proposed that male fitness would be increased enough by reducing the generation time (assuming that smaller plants were younger) to compensate for lower survivorship when males reproduced at smaller sizes. An alternative argument is that as long as male reproductive effort is less than that of females, males ought to be able to reproduce at a smaller size than females, without incurring any greater risk. Thus, it would be interesting to compare the survival rate of the smallest males, to that of larger males. Examining the survival data for *V. edulis* by size class showed that the lowest survival did occur in the smallest size class for males. (Interestingly, the lowest survival for females was in the largest class.) Although the number of plants dying were too few to draw conclusions, this suggestion of risk to small males is intriguing and merits attention in future studies.

Apart from returning to the field for more data from marked plants, a method is available which would help unravel this problem. By modeling the population dynamics of this species incorporating the sex differences in life histories found here, and then manipulating key factors, the effects of differential survival and age of maturity on population size structure and sex ratio can be determined. The effects on male fitness of reduced age of reproductive maturity with and without concurrent reduced survivorship can be explored, and the assumptions behind Melampy and Howe's proposal can be detailed. Portions of this work will be taken up elsewhere (Chapter 4).

Trade-offs Between Growth, Survival and Reproduction

The fact that no consistent difference between the average male and female growth rate was found, despite a higher reproductive allocation by females, indicates that a simple trade-off between reproductive allocation and growth allocation does not occur in *Valeriana edulis*. Few data are available in the literature for comparison; only a handful of studies have compared growth rates of the sexes, only three other studies to date have reported reproductive effort for males and females of dioecious species, and only one other study included both measurements (Gross and Soule, 1981). In *Silene alba* female reproductive effort was greater than male as long as females achieved at least 20% fruit set, but males and females grew to the same size during the course of the study, indicating similar growth rates. Again, no trade-off between reproductive allocation and growth occurred (Gross and Soule, 1981). Chamaelirium luteum also showed no difference between the sexes in growth, even though flowering plants of either sex grew less than nonflowering plants (Meagher and Antonovics, 1981). Unfortunately, no comparable measure of reproductive effort was made for this species.

Studies reporting differences between male and female growth rates of dioecious species have generally found (or implied) that male growth rates exceed those of females in perennial species, but that the reverse is true in a number of annual or short-lived perennial species. Lloyd and Webb (1977) include a thorough review of this subject. One case in which this pattern does not hold is Populus tremuloides, a woody perennial, recently reported to have higher female than male growth rates (Grant and Mitton, 1979). Apparently, depending upon the species, either sex may have the higher growth rate.

So far no case has been found where total female reproductive effort (including seed set) is lower than male reproductive effort. In addition to the present study and those on Silene alba (Gross and Soule, 1981) and Fragaria chiloensis (Hancock and Bringhurst, 1980), higher female reproductive effort was found in Rumex acetosella (Putwain and Harper, 1972), and also in Simmondsia chinesis, as long as females achieved at least 30% seed set (Wallace and Rundel, 1979).

If it is generally the case that female reproductive effort is greater than male, then higher female growth rates cannot be explained by a trade-off with reproductive expenses. It seems that there is solid evidence in a number of cases that allocation of resources to reproduction is not negatively related to allocation to growth, and little hard evidence that there is a trade-off.

Note that average growth rates in both sexes of Valeriana edulis declined with increasing plant size. This same pattern occurs in Chamaelirium luteum (Meagher and Antonovics, 1981), a dioecious perennial forest herb. As in V. edulis, C. luteum also shows an average negative growth from one year to the next for the largest plants. The negative average growth rate of large plants of V. edulis conceals a higher average growth rate among the large plants with positive size changes. Thus size changes, whether negative or positive tend to be more extreme in large plants than small. To get an accurate picture of the population dynamics of this species, it would be useful to be able to separately categorize large growing and large senescing plants. This would be difficult to do in an unbiased manner (other than assuming that all shrinking plants are "senescent"). One potential method that could be applied in future studies would be to use some measure of leaf cover (e.g., a combination of leaf number and plant diameter) to categorize plants, as sensecent plants seem to have sparser leaf cover (personal observation).

Growth rates fluctuated dramatically from one year to the next for individual plants, for each sex, and for each size class. Growth rates may be sensitive to seasonal growing conditions, but because sometimes females reacted one way and males another to the same set of environmental conditions, it is difficult to interpret seasonal effects. Certainly microsite differences and herbivory also contribute to individual variation from year to year. The magnitude of year to year variation found in this study makes it clear that it is necessary to be cautious about generalizing from this data set. Data from more seasons, and perhaps more detailed classification of plants (e.g., developing a "senescent" class) are needed before definitive comparisons of growth in males and females can be made. Growing plants under controlled conditions would also be desirable, but any patterns found in such a study would have to be interpreted in light of natural variation found in the field.

Analysis of growth in plants classified into "flowering-year" and "preflowering-year" categories suggested that during a flowering year, growth rates may be reduced. This pattern was only statistically significant in the second season of growth, but the mean values appeared to differ in the same direction in the first season of study. Thus, in some years there can be an apparent trade-off between growth and reproduction in *V. edulis*, at least in certain subgroups of plants. *Chamaelirium luteum*, a dioecious forest herb, also showed a reduction in growth during a flowering year compared to growth during the year after flowering (Meagher and Antonovics, 1981; note that Meagher's data is classified slightly differently than mine because his plant size measurements were made at the end of the season, whereas mine were made near the beginning of the season.) One difference stands out between *V. edulis* and *C. luteum*: in *C. luteum* females show a greater reduction in growth during flowering than do males, whereas in *V. edulis* the growth reduction is about equal in females and males. The data for *C. luteum* indicate a trade-off between growth rate and reproduction, and the greater effect in females suggests greater reproductive expenses in females. However, overall male growth did not differ from overall female growth. In contrast, in *V. edulis* the suggested trade-off between growth and reproduction is not consistent from year to year and is probably not tight enough to compensate for consistently higher reproductive costs of females.

A very clear trend emerged from the analysis of growth in plants classified by number of flowering episodes over a three year span: the more often a plant flowered, the more it grew. This relationship is again in contrast to data on *Chamaelirium luteum* which showed that the more often a plant flowered, the less it grew (Meagher and Antonovics, 1981). In *V. edulis*, growth can be interpreted as a measure of plant vigor, such that the more vigorous a plant, the more it flowers, on average; however, each individual plant grows less during the year it flowers than during a resting year. Thus rather than seeing growth as an optional expense which can be exchanged for flowering, growth may be a prerequisite for flowering. This could be a simple constraint of the growth form of *V. edulis*; perhaps only new buds at the crown can produce inflorescences. It would be informative to compare the pattern of placement of inflorescences in *V. edulis* and *C. luteum*.

This positive correlation between growth rates and flowering frequency may indicate microsite quality differences among plants, such that plants in the best microsites can both grow and flower more than those in poorer sites. Microsite may be a significant component of variance in analyses comparing male to female growth rate and could potentially mask real differences between the sexes. Further, the sexes may differ in frequency of occurrence in different quality microsites, again making it difficult to detect real differences in growth potential of the sexes from simple field surveys. For instance, if females tend to occur in better microsites than males, and to have lower growth rates than males in equivalent microsites, the result of a field comparison might be no difference in the average growth rate of males and females. In order to separate a possible effect of microsite on growth rate from possible differences between the sexes in growth rate, it would be desirable to set up an experiment in which cloned individual males and females were grown under a variety of uniform conditions. Such a technique is feasible for a plant with a growth form like V. edulis, and has recently been successfully used with another species to detect differences between the sexes that were not discernable in the field (D. C. Freeman, personal communication).

The significant point emerging from this portion of my study is that males and females of Valeriana edulis differ in reproductive allocation, but not in growth rates. Despite the fact that for the average plant, growth rate is lower during a flowering year than during a resting year, no difference was found between males and females in this response. Higher reproductive effort in females than males is partially compensated by lower probability of flowering in females than males, but no further compensation in growth rate is seen.

Survival rate date did not show any significant difference between males and females; however, the survival rates were high and estimates were of necessity based on the few plants which died (a total of only 14 males and 15 females died over the two years of study). These data alone cannot refute a hypothesis of unequal survival between the sexes. At such high survival rates it would take a sample size of 1300 plants to detect even so large as a 10% difference between the sexes at a 5% significance level (e.g., if true survival rates were actually 0.95, and 0.85). Fortunately the size distribution data, based on large samples, also suggests equal survival of males and females. Given that on the average, growth rate is equal in the sexes, size will be a correlate of age. Then, if one sex did survive at a lower rate, proportionately fewer plants of that sex would reach the largest size class. The fact that this does not occur, that the size distributions are very similar in males and females, is good evidence that survival rates are on the average, equal.

Only one other study to date includes measurement of survivorship obtained in the field from marked males and females. Meagher and Antonovics (1981) found that female survival was generally lower than male survival in Chamaelirium luteum. Apart from these data there is only indirect evidence of survival rates of males and females in dioecious plants, such as biased sex ratios, or differences in hardiness with respect to some environmental conditions (see Lloyd and Webb, 1977; and Soule, 1981a, for reviews of this literature). In most of these cases, females appear to have lower survival than males, and some authors have concluded that higher male survival is a direct consequence of a lower cost of reproduction in males (Darwin, 1877; Lloyd and Webb, 1977; Meagher and Antonovics, 1981).

It is apparent from the present study that neither differential survival, nor differential growth are necessary consequences of differential reproductive expenses. This study, as well as that of Grant and Mitton (1979) which found consistently higher radial growth rates in female clones than in male clones of Populus tremuloides, suggest that the notion of resource allocation trade-offs between reproduction, growth, and survival may be too simple even to describe the differences in life history features between members of a single population. While resource allocation is still a useful conceptual tool, it should be used with care. It is apparent from this and other studies that expected consequences (e.g. differential mortality) cannot be assumed on the basis of documentation of different resource allocation patterns alone.

The Pattern and Mechanism of Sexual Differences in *Valeriana edulis*

In summary, these data support the commonly held notion that male reproductive effort is lower than female per reproductive episode. For *Valeriana edulis* this difference is mainly due to the fact that seed production is confined to females. Resource allocation trade-offs with survival and growth rate apparently do not occur. Instead, differences in resource allocation between the sexes has had primarily two consequences in *V. edulis*: smaller size at reproductive maturity, and higher reflowering rates in males. Thus, trade-offs are entirely within the reproductive function, rather than between reproduction and growth or survival. It appears that costs of reproduction are in effect delayed to the following season, and occur in the form of influencing the chance of flowering again. In contrast, a plant such as *C. luteum* (discussed above; Meagher and Antonovics, 1981), experiences immediate effects of the proportion of resources allocated to reproduction during each flowering season, showing a greater decrease in growth rate by flowering females compared to non-flowering females than do males, and a lower survival in females compared to males.

By what mechanism a plant such as *V. edulis* delays the effect of flowering is an intriguing question. It may be related to the particular growth form of the plant. Possibly, the large storage tap root of *V. edulis* acts as a reservoir that is drawn upon for flowering, somewhat independently of growth and maintenance. By analogy, one could think of a special container only for flowering resources within the tap root, which must be filled to a certain level before flowering can occur. Since each female flowering episode takes more resource than a male's, it takes longer for the female's container to refill. Hence, females have a lower flowering frequency. Additionally, the threshold of fullness could be lower for males, explaining the higher frequency of males flowering at small sizes. Whatever the mechanism, it seems clear that growth form has interacted with other life history features during the evolution of dioecy in *V. edulis*. In order to understand the evolution of differences between the sexes in dioecious plants it is necessary to consider both growth form and life history.

CHAPTER 3

FACTORS INFLUENCING ADULT SEX RATIO IN THE DIOECIOUS PLANT, VALERIANA EDULIS NUTT.

INTRODUCTION

When males and females of dioecious plants differ in certain life history characteristics, the observed adult sex ratio is influenced. In particular, when survival and age of maturity differ for the sexes, the proportion of each sex in the adult population is affected. In addition, in iteroparous species the expressed sex ratio (ratio among plants flowering in a given season) may differ from the basic sex ratio (ratio among all plants of reproductive age or older whether in flower or not) if the flowering frequencies of the sexes differ. Since plants can be sexed easily only when in the flowering state, it is not readily apparent whether these two ratios are equivalent (unless all plants are in flower). Differences between the sexes in these critical life history traits have been predicted based on theory of sexual selection and the concept of resource allocation (Chapter 2), and in many dioecious plants the sexes do differ in one or all of these traits.

Studies of dioecious plants have often reported adult sex ratios widely divergent from the expected value of 1:1 for the primary sex ratio (Godley, 1964; Lloyd, 1973; Lloyd, 1974). But few studies have attempted to trace the source of deviation, whether it be from the primary sex ratio, differential survival, or age of maturity, and most have failed to distinguish expressed sex ratio (ESR) from basic sex ratio (BSR). Those who did investigate the cause of the biased adult ratio have found two common patterns. For plants which show male-biased adult sex ratios, there are often indications that male survivorship is higher, at least among reproductives (Lloyd, 1973; Lysova and Khizhnyak, 1975; Onyekwelu and Harper, 1979; Webb and Lloyd, 1980; Meagher, 1981a), or that males mature earlier (Clark and Orton, 1967; Opler et al., 1975; Opler and Bawa, 1978; Meagher, 1981a). For plants which show female-biased adult sex ratios, there are usually indications that the female-bias exists prior to adulthood, perhaps in the primary sex ratio (Lloyd, 1974; Rychlewski and Zarzycki, 1975; but see Putwain and Harper, 1972). Recently, higher female survivorship (Zarzycki and Rychlewski, 1972; Grant and Mitton, 1979; also, Correns, 1923, referenced in Putwain and Harper, 1972), and/or different ages of reproductive maturity (Melampy and Howe, 1977) have also been implicated in cases of female-biased ratios.

Presented here are results of a study of those factors which may affect the adult sex ratio in Valeriana edulis, a long-lived iteroparous dioecious herb, native to the North American Rocky Mountains. Adult sex ratios, both expressed (ESR) and basic (BSR), are compared in four study populations and ESR recorded in an additional 11 populations. Differential survival, size at reproductive maturity, and flowering frequency of the sexes are obtained from each of the four main populations (see Chapter 2 for a comparison of these and other traits at the species level for V. edulis). Environmental factors which could influence any of the above are also explored. For this study the primary sex ratio was not obtained, but future studies will attempt to do so by germinating seeds, and growing resultant plants to adulthood, while attempting to maintain 100% survivorship. If it is found that V. edulis has identifiable sex chromosomes, it might also be possible to identify seedlings by sex through chromosome counts. For the present, this evaluation of factors affecting the sex ratio during adulthood will provide information about the sex ratio of plants just entering the adult stage, and from this, some inferences about sex ratio prior to adulthood are possible.

METHODS

Valeriana edulis is a long-lived iteroparous, herbaceous species growing in open areas throughout the Rocky Mountains. For description of the species, see Chapter 2. Fifteen populations were sampled within a 10 mile radius of the Rocky Mountain Biological Laboratory, near Crested Butte, Gunnison County, Colorado. Of these, four were chosen for more intensive study: Brush Creek Pasture (BCP), Brush Creek Range (BCR), North Rustler's Gulch (NRG), and Bellview I (BI). Table 3-1 lists various characteristics of these four populations and sites.

Expressed sex ratio was recorded in the field by censusing all plants within a large, measured area until either at least 100 flowering plants were censused or all plants were censused. Census areas ranged from over 2000 m^2 down to only 200 m^2 in the most dense, restricted populations, with most populations well over 700 m^2 sampled. At each census I recorded whether each plant was vegetative or flowering, and if the latter case, their sex. Basic sex ratio was calculated for the four study populations from the ESR and flowering frequency. In each population, 150 plants (50 male, 50 female, and 50 vegetative) were marked and monitored for three consecutive years beginning in 1978. In 1979 in three populations excluding BCP,

Table 3-1: Description of four main study sites and populations of *Valeriana edulis*; BI = Bellview-I; NRG = North Rustler's Gulch; BCR = Brush Creek Range; BCP = Brush Creek Pasture.

Population	Altitude	Aspect	Plants/m^2	Average Plant Size[1]	Average % Males[2]
BI	3462	W	0.76	13.18	30.92
NRG	2987	S40E	1.12	10.36	34.21
BCR	2755	S10W	3.06	10.22	38.02
BCP	2755	S10W	2.37	4.27	46.45

[1] Diameter at crown-leaf bases

[2] Flowering plants only (expressed sex ratio)

additional plants were marked and thereafter also monitored. These plants were contained in rectangular grids within which all plants were marked. The total number of plants marked in both years was 150 in BCP, 273 in BCR, 298 in NRG, 244 in BI. The average flowering frequency of plants of each sex was calculated for each standard size class[1] (diameter at root crown) as follows:

flowering frequency (or probability of flowering),

$$P(fl)_i = \frac{(N_1 X 1) + (N_2 X 2) + (N_3 X 3)}{3(N_1 + N_2 + N_3)},$$

where, N_1 is the number of plants flowering once in 3 years, N_2 is the number that flowered twice in three years, and N_3 is the number that flowered three times, and i = size class. The total number of males (both flowering and vegetative), =

$$T(male) = \text{number of males flowering}/P(fl).$$

The total number of females, T(female) is calculated similarly. The value of T for males and for females are used to calculate the basic sex ratio of the population,

$$BSR = \frac{T(male)}{T(female) + T(male)}.$$

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[1] Standard size classes were calculated independently for each population by the method proposed by Vandermeer (1978) for figuring appropriate size classes for a stage projection matrix population dynamics model. Division of populations into size classes gives a more accurate estimate of characteristics that are dependent on size, such as flowering frequency and growth rate. Size-specific rates were multiplied by the proportion of the population falling in each category to obtain overall averages (see Soule, 1981d for listing of size classes for each population).

ESR and BSR were compared with chi-square contingency tests, and interpopulation heterogeneity was tested (again with chi-square tests) for both ESR and BSR.

Survival of the marked individuals was monitored in each population in each succeeding season following marking. A second method of comparing survival of males and females is to look for a difference in the age distribution of the sexes, indicative of differing probabilities of attaining each age, i.e., differing survival rates. In this case, size, rather than age distributions were compared, because growth rates recorded on marked plants from 1978 to 1980 did not differ between the sexes in any of the populations (Table 3-2), and because plants cannot be aged directly. With growth rates equivalent in males and females, the relationship of size to age and to survival is the same for each sex. Size distributions of males and females were compared in each population by means of a Kolmogorov-Smirnov goodness of fit test (Sokal and Rohlf, 1969).

In Valeriana edulis the average size of males and females at reproductive maturity is indicative of the relative age at maturity, (because growth rates are similar in males and females). This size was estimated for each sex in all four populations by determining the size below which 90% of all flowering plants showed no evidence of ever flowering previously (see Chapter 2 for a more detailed description and discussion of this criterion).

If males and females differ in average size at maturity, this will tend to increase the frequency of the sex which matures earlier (smaller). For this effect to influence the overall sex ratio of a population, a large proportion of that population must fall in the size

Table 3-2. Growth Rates: Results of analysis of variance for size and sex effects on growth rates in 4 populations of *Valeriana edulis*.

	Significance Level		
	Size Effect[a]	Sex Effect	Interaction
BCP	n.s.	n.s.	n.s.
BCR	**	n.s.	n.s.
NRG	n.s.	n.s.	*
BI	n.s.	n.s.	n.s.

[a] Standard size classes

n.s. = not significant, $p < 0.05$

* $P < 0.05$ $F_{int(NRG)(3,93)} = 3.88$

**$P < 0.01$ $F_{size(BCR)(3,86)} = 4.59$

range containing mainly plants flowering for the first time. A minimum size of flowering was found for each population by determining the size below which at least 90% of all vegetative plants had not previously flowered. Then the proportion of each population falling within this size range was calculated. This size was as small or smaller than the average size at maturity of each sex already described with the exception of males in NRG.

A number of environmental, or population characteristics were measured for the four main populations, and for six minor study sites. Environmental factors measured included altitude, obtained from topographic maps, aspect, determined with a compass, and simple soil moisture, measured using a soil moisture meter (O.S.K., E.M. System Soil Tester) which measures "% soil moisture". A measure of relative water stress, "leaf hydration", designed after Marchand and Chabot (1978), was used in conjunction with soil moisture measurements in the four main populations. Leaf hydration was measured as the wet weight of fresh leaves divided by the wet weight of saturated (hydrated) leaves, so it is a measure of how close leaves are to saturation. Leaves were collected in the field from 10 pairs of adjacent male and female plants, immediately placed in individual zip-loc plastic bags, sealed, stored on ice in a cooler for up to an hour during transport to the lab, then weighed in the sealed bags. Then leaves were floated in water in open plastic bags for at least 24 hours, before reweighing (subtracting bag weight), to obtain saturation weight. Collections were made during the driest part of the season, in the afternoon (at time of greatest water stress), twice at each of BCP, BCR, and NRG, and once at BI (it began to rain daily on the day following the single collection at BI). Intensity of grazing by livestock was noted in all ten populations, and the number of other common plant species was also recorded in the four study populations. Population density and average plant size (basal diameter, see Chapter 2) were obtained from field censuses in each population.

RESULTS

Adult sex ratio among flowering individuals (ESR) of *Valeriana edulis* is generally female-biased, and usually ranges from 30% to 50% males with an average value of 38% (Table 3-3). The average ESR is significantly different from 1:1 in 12 of the 15 populations (all but the three with the highest proportion of males). There is significant heterogeneity among populations (X^2 contingency analysis on 10 populations listed in Table 3-9; X^2 - 51.82**, df 9, $p < 0.01$), and this variation among populations cannot be explained as simple random variation around the average ESR. An analysis of goodness of fit of the distribution of expressed sex ratios of the 15 populations to the normal approximation of the binomial showed significant deviations at both tails of the distribution (Table 3-4). Of the 15 populations, two had sex ratios less than 30% male, and another three had sex ratios greater than 45% male, both ranges with a probability of less than one percent of finding a value so extreme. Of the four intensive study populations one had extremely high and one extremely low biased sex ratios (BI and BCP) and two had values near the average (NRG, BCR).

Table 3-3 also shows the ratio of flowering/vegetative plants for ten of the populations. There is a significant positive relationship between the proportion of the population that is vegetative and the

Table 3-3. Sex ratio and proportion of plants not in flower in 15 populations of *Valeriana edulis* Nutt. ESR is % males among flowering plants; F is the number of flowering plants in the sample area; V is the number of vegetative plants in the sample area. Asterisks indicate the four main study populations.

	1978			1979			1980		
POPULATION	ESR	F	V/F	ESR	F	V/F	ESR	F	V/F
EMERALD LK.	25.66	491	0.41	28.19	118	0.56	-	-	-
* BELLVIEW I	29.80	198	0.93	36.76	68	0.87	29.33	111	0.52
THAL. HILL	33.62	235	0.47	34.21	152	0.82	-	-	-
* N. R. GULCH	29.90	311	0.64	38.74	222	0.54	38.89	72	0.76
BELLVIEW II	34.90	298	5.28	33.91	115	3.48	-	-	-
C. B. CEMETERY	35.58	332	-	34.90	192	1.00	-	-	-
MT. C. B.	35.50	231	-	-	-	-	-	-	-
HAYSTACK	36.79	386	-	34.27	248	0.48	-	-	-
* B. C. RANGE	39.83	231	1.16	31.88	140	1.48	48.78	41	2.41
E. R. BRIDGE	38.71	31	0.26	-	-	-	-	-	-
N. MT. C. B.	41.60	125	-	-	-	-	-	-	-
SLATE RIVER	42.10	266	-	-	-	-	-	-	-
* B. C. PASTURE	46.96	247	2.02	45.68	162	1.67	-	-	-
CATTLEGUARD	47.06	119	0.30	43.71	151	0.23	-	-	-
B. C. COWCAMP	48.82	254	-	-	-	-	-	-	-

Table 3-4. Distribution of sex ratios in *Valeriana edulis*; comparison of distribution of observed sex ratios to a normal approximation of the binomial distribution, with mean, $p = 37.79$, and standard deviation, $\sqrt{pq/n} = 3.067$.

Population	Average % Male	Z calc	Probability of a more extreme value
Emerald Lk.	26.15**	-3.80	0.0001
+Bellview I	30.92*	-2.24	0.012
Thal. Hill	33.85	-1.28	0.100
+N.R. Gulch	34.21	-1.17	0.121
Bellview II	34.62	-1.03	0.152
C.B. Cemetery	35.33	-0.80	0.212
Mt. C.B.	35.50	-0.75	0.227
Haystack	35.80	-0.65	0.258
+B.C. Range	38.02	-0.07	0.472
E.R. Bridge	38.71	0.30	0.382
N. Mt. C.B.	41.60	1.24	0.108
Slate River	42.10	1.40	0.081
+B.C., Pasture	46.45**	2.82	0.002
Cattle guard	45.19**	2.41	0.008
B.C. Cowcamp	48.82**	3.60	0.0002
Overall p =	37.79		

+ indicates four main study populations

* P < 0.05 of obtaining a sex ratio so extreme

**P < 0.01 of obtaining a sex ratio so extreme proportion of flowering plants which are male (Figure 3-1); i.e., the ESR varies directly with the proportion of the population that is vegetative. Relatively more males are seen flowering in populations where many plants are currently vegetative, and more females in populations with most plants currently flowering. This could be explained in at least two ways. First, all populations could actually have the same percentage of males and females among all adults, but have differing proportions of males and females in flower. An alternative is that the actual percentage males varies simultaneously with the percentage of plants flowering, and both vary in concert with some other causal variable. One question of interest is whether the differences in sex ratio among populations is simply a matter of differences in male and female flowering patterns, or whether the proportion of males among all adults (both flowering and vegetative) also differs. That is, does the ESR equal the BSR in these populations? If BSR's differ among populations, sexual differentiation of survival rates, age of maturity, or variable primary sex ratio is implied, whereas if only ESR's differ, it is possible that only the flowering patterns of the sexes differ among populations with differing ESR's.

Table 3-5 shows the calculation of BSR from the ESR and the probability of flowering for the four populations. BSR did not differ significantly from ESR within any of the populations. In all cases, the BSR showed a higher percentage of females than the ESR, since female flowering frequency is consistently slightly lower than males (Chapter 2). Nevertheless, the difference between ESR and BSR was not related to the proportion of the population flowering per season, and

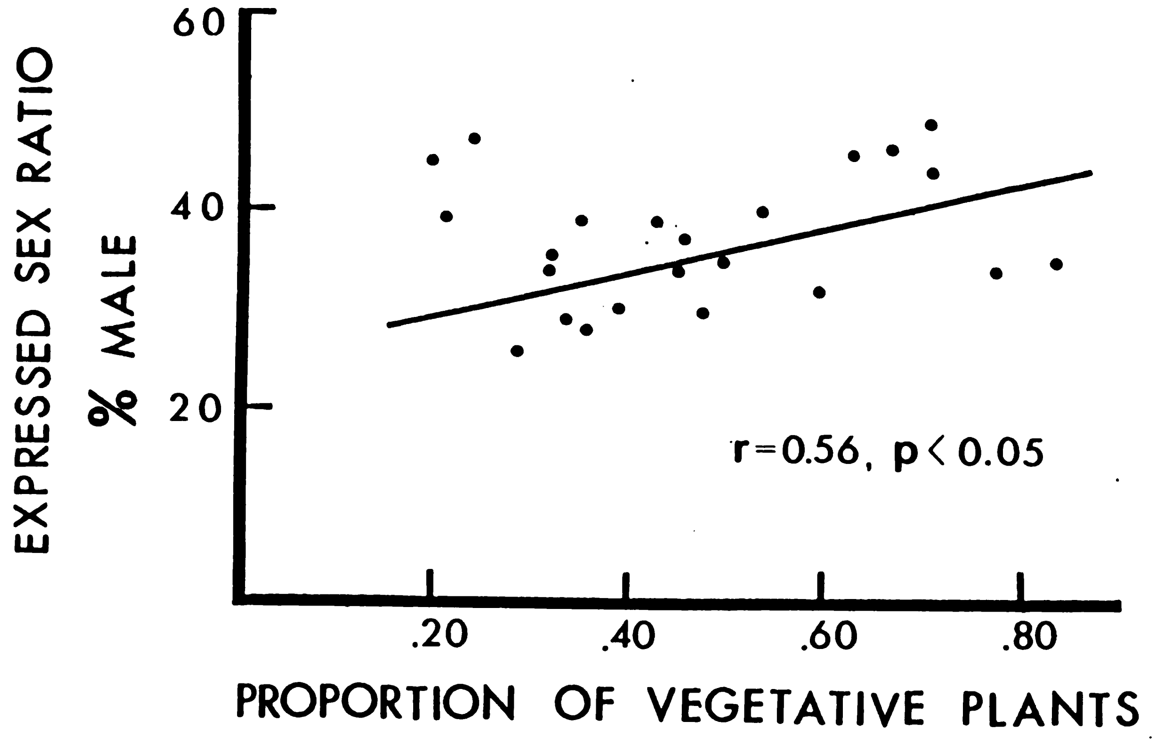

Figure 3-1: Relationship between proportion of population flowering and the percentage males among flowering plants (ESR) in *Valeriana edulis* Nutt. Each point represents a single sample from one of fifteen populations (see Table 3-3).

Table 3-5. Basic and expressed sex ratios in four populations of *Valeriana edulis* Nutt.

		BCP	BCR	NRG	BI
$\bar{x}$ ESR (% male)		46.45	38.02	34.21	30.92
# FLOWERING	M	190	157	207	117
	F	219	255	398	260
†PROBABILITY OF FLOWERING	M	0.5500	0.5889	0.8752	0.8037
	F	0.5303	0.5773	0.7649	0.7138
CALCULATED TOTAL # OF ADULTS	M	345	266	236	146
	F	413	442	520	364
ESTIMATED BSR (% male)		45.51	37.57	31.22	28.63
% REMAINING UNSEXED		2.69	7.33	2.00	4.00

† independently derived

X^2 for ESR vs. BSR	0.16	0.04	2.49	1.05
X^2 for BSR = 50.00	3.35*	33.80**	85.17**	68.76**

X^2 for heterogeneity of ESR's among populations = 23.46***

X^2 for heterogeneity of BSR's among populations = 86.09***

* $p < 0.05$, $X^2_{0.05}$, 1 df = 3.84

** $p < 0.01$, $X^2_{0.01}$, 1 df = 6.63

***$p \ll 0.01$, $X^2_{0.01}$, 3df = 11.34

BSR as well as ESR differs significantly among populations. This means that the actual percentage males does vary simultaneously with the percentage of plants flowering (the second alternative, above).

Table 3-5 also reports the proportion of the population still remaining unsexed at the end of the study. In no case is this great enough to account for the bias in BSR away from 50% males (with the possible exception of BCP). Apparently, both the interpopulation differences in sex ratio, and the tendency towards female bias are distinct phenomena in Valeriana edulis.

Survival Rates of Males and Females

Comparing the relative survival rates of males and females among the four populations there is a striking trend from higher male than female survival, to higher female than male survival as the percentage males across populations declines (Table 3-6). The correlation coefficient is 0.981, 2df, $p < 0.05$, and the X-intercept of the associated regression is 37.95, very close to the mean sex ratio from 15 populations (37.79, Table 3-4). This implies that even when adult survival rates of males and females are equal, the adult sex ratio is female-biased (only 38% male). Conversely when adult survival rates of males and females are not equal, the adult sex ratio is correspondingly more or less female-biased. However, only in population BI was the difference between the survival rates of the sexes significant.

Comparing the size frequency distribution of the sexes for each population (Fig. 3-2a-d) there was only one significant difference between the sexes, in the 13-14 cm size class in population NRG ($D_{0.05} = 12.86$). The significantly higher frequency of males in these

Table 3-6. Survival rate of males and females of *Valeriana edulis* from four populations

POPULATION	#deaths/#observations* MALES	FEMALES	% surviving MALES	FEMALES	relative survival (MALE-FEMALE)[1,2]	basic sex ratio
BCP	6/63	11/83	90.48	86.75	+3.73	45.51
BCR	3/83	3/89	96.38	96.63	-0.25	37.57
NRG	3/94	1/149	96.81	99.33	-2.52	31.22
BI	6/82	2/123	92.68	98.38	-5.76	28.63

[1] X^2 test for significant difference between male and female survival significant only in BI: BI $X^2 = 4.25^*$, 1 df, $p < 0.05$

[2] $r = 0.981^*$, 2df, $p < 0.05$ for correlation between relative % surviving and BSR

* number of plants years observed

Figure 3-2: Size distributions of males and females in four populations of *Valeriana edulis* Nutt. D_{max} is Kolmogorov-Smirnov test statistic; * indicates significant value at $P < 0.05$. a) - d) indicate the four populations; .... = female; ——— = male.

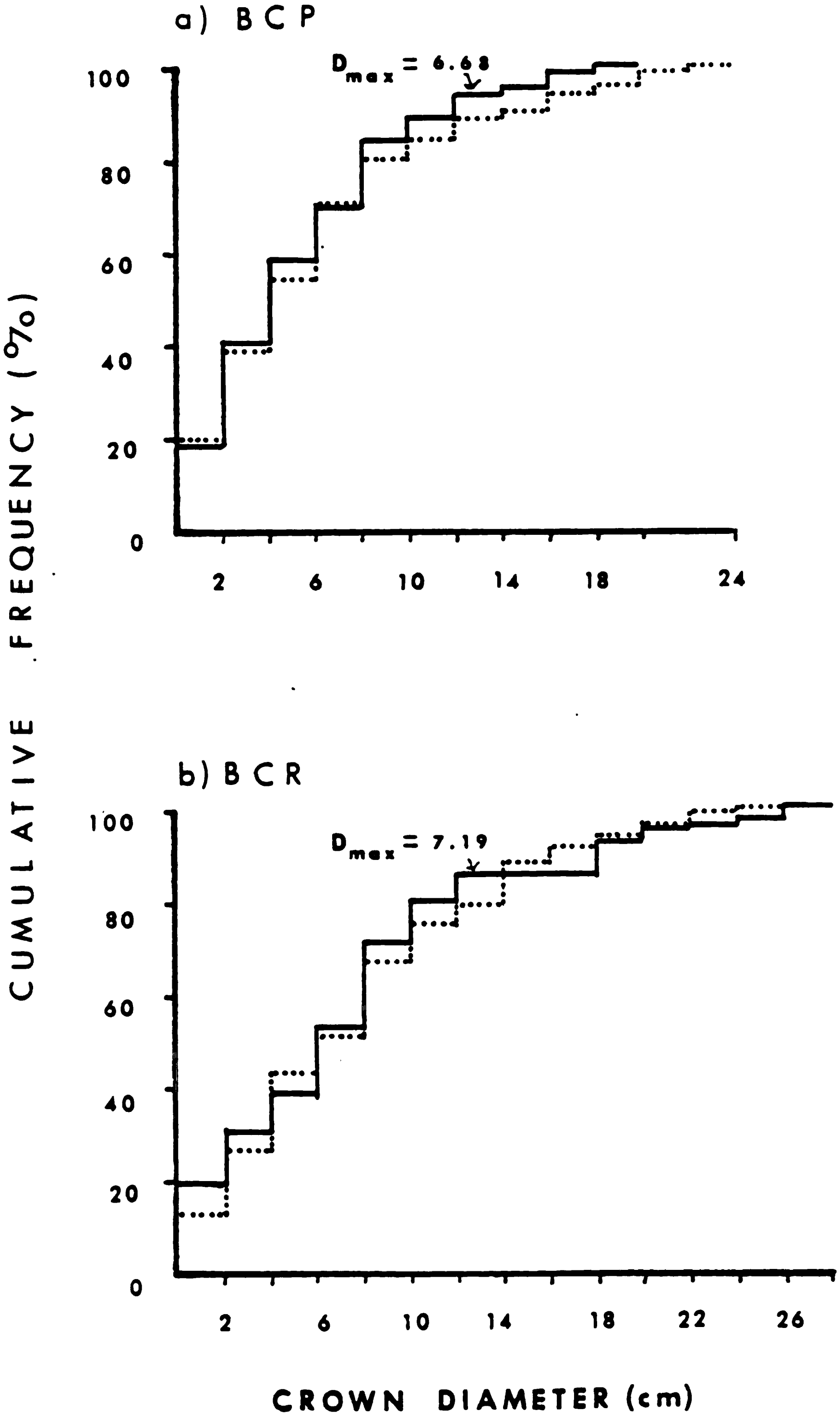
a) BCP
$D_{max} = 6.68$
100
80
60
40
20
0
2
6
10
14
18
24
b) BCR
$D_{max} = 7.19$
100
80
60
40
20
0
2
6
10
14
18
22
26
CUMULATIVE FREQUENCY (%)
CROWN DIAMETER (cm)

Figure 3-2

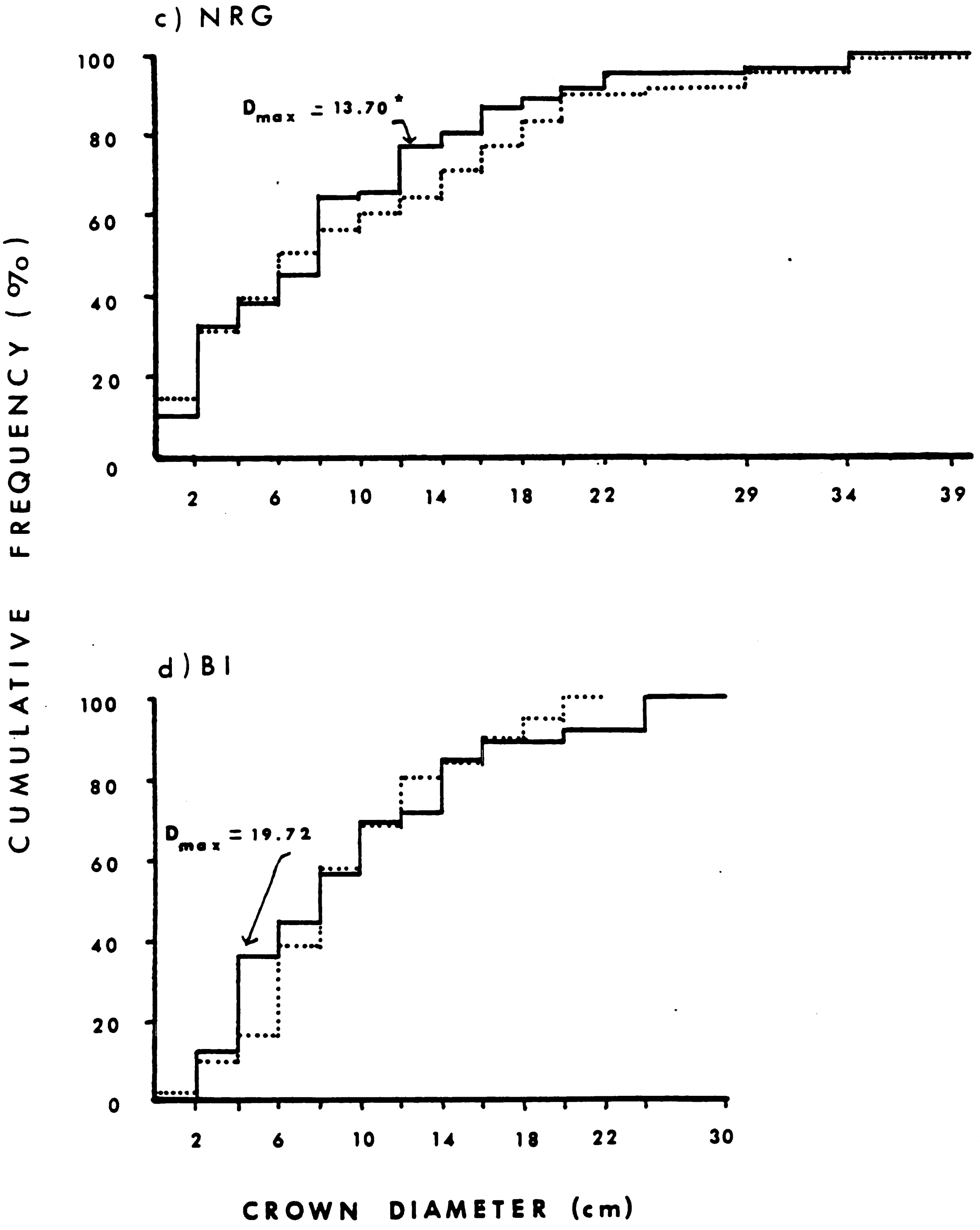

Figure 3-2, continued

intermediate-sized plants in this population suggests a higher survival rate of females than males, since a greater proportion of the females reach the larger sizes. In direct survival comparisons (Table 3-6) female survival in NRG appeared to be greater than male, but the difference was not significant. In population BI, in which female survival is significantly greater than male (Table 3-6), the size distributions of males and females did not differ significantly, although D_{max} was close to the critical statistical value (D_{max} = 19.72, $D_{0.05}$ = 23.29). In this case, the greatest difference in the frequency of sizes of males and females was in small plants (5-6 cm), with males again more frequent than females. This type of size pattern has been interpreted as meaning a larger average size of reproductive maturity for females than males (Opler and Bawa, 1978).

Size at Reproductive Maturity

The estimated average sizes at reproductive maturity were quite close for males and females in all populations (Table 3-7), with a maximum difference of 2 cm in population NRG and a minimum of 0 cm in population BI. In all three cases where the size estimates differed for the sexes, the male size was smaller than that for females, which should tend to elevate the percentage of males among the smallest plants.

However, few plants (20% or less of populations) were involved in the category of smallest flowering plants (Table 3-7). Consequently, a male-biased sex ratio among these plants has little impact on a population's overall sex ratio.

Environmental Correlates of Sex Ratio

Comparing several environmental factors and population

Table 3-7. Estimated size at reproductive maturity of males and females in four populations of *Valeriana edulis* Nutt. (See text for description of methods.)

POPULATION	SIZE (cm) MALES	SIZE (cm) FEMALES	RELATIVE SIZE (MALE - FEMALE)	% OF POPULATION ≤ MFS
BCP	4	5	-1	20%
BCR	3	4	-1	13%
NRG	2	4	-2	17%
BI	3	3	0	9%

characteristics for the four main study populations, (Table 3-8) several trends are apparent: the proportion of males appears to decline with increasing altitude, decreasing grazing intensity, decreasing population density, increasing plant size, and decreasing soil moisture. For *V. edulis* these apparent differences in soil moisture are probably not highly biologically significant, since plant water-stress measurements (% leaf hydration, column 6, Table 3-8) taken at the same time as soil moisture readings did not follow the same pattern. The other abiotic factors, altitude and aspect, show no relationship to sex ratio in the six minor populations. Considering all ten populations, correlations between ESR and altitude, population density, and average plant size were not significant. Thus, no conclusions about the importance to sex ratio of trends in these factors for the four study populations can be made with certainty.

DISCUSSION

Sex Differences in Survival and Adult Sex Ratios

Valeriana edulis shows an overall tendency toward female-biased adult sex ratios, averaging about 38% males. Evidence from this study suggests that this female bias is present prior to the onset of reproductive maturity. Where male and female adult survival rates were most nearly equal (population BCR) the ESR was also closest to the overall average of 38% male. Where male and female survival rates apparently differed (populations BCP, NRG and BI), adult sex ratios were either higher or lower, dependent upon whether males or females had the higher survival rate, respectively.

Only a few documented cases of the effect on sex ratio of

Table 3-8. Environmental and population characteristics, and sex ratio in *Valeriana edulis* Nutt.
a) Four main study sites; b) Six minor study sites.

	POPULATION	AVERAGE ESR	ALTITUDE	ASPECT	GRAZING[1]	POP. DENSITY	PLANT SIZE (x)[3]	MIN. SOIL MOISTURE %	MIN.LEAF HYDRATION	#COMMON PLANT SPECIES
a)	* BI	30.92	3462m	W	[b]none to rarely heavy	$0.76/m^2$	13.18	5.0±2.1	85%	13
	*NRG	34.21	2987	S 40 E	none	1.12	10.36	1.0±0.7	81%	13
	*BCR	38.02	2755	S 10 W	[a]medium	3.06	10.22	38.0± 7.9	86%	9
	*BCP	46.45	2755	S 10 W	[a]heavy	2.37	4.27	34.5±3.6	79%	13
b)	EM. LK.	26.15	3194m	N 20 W	none	$0.35/m^2$	11.81cm	1.0±1.0		
	THAL. HILL	33.85	2902	N 70 W	[a]light	0.38	15.99	-		
	BELL II	34.62	3395	N 50 W	[b]none to rarely heavy	0.44	6.54	-		
	C.B. CEM.	35.33	2700	S 25 W	none	>0.15[2]	11.02	22.3±6.0		
	HAYSTACK	35.80	2755	S 25 W	cut for hay	>0.47[2]	12.77	54.9±2.5		
	CATTLEGUARD	45.19	2926	N 70 E	[a]none to light	0.03	11.69	30.3±5.9		

differential survival of males and females in dioecious plants appear in the literature. The best documented case to date found generally higher male survival, and male-biased sex ratios in Chamaelirium luteum (Meagher 1981a, Meagher and Antonovics 1981). In cultivated fields, males of Asparagus officinales have higher survival rates than females, and sex ratios in older populations tend to become progressively more male-biased with time (refs. in Lloyd and Webb, 1977). In experimental populations of Rumex acetosa, Silene alba, and S. dioica, males had lower survival rates than females (Correns, 1928, ref. in Lloyd and Webb, 1977). All three of these species have been reported to have female-biased sex ratios in natural populations although some biasing may occur prior to maturity (Putwain and Harper, 1972; Zarzycki and Rychlewski, 1972; Lloyd, 1974). Cases where differential survival was inferred from size distributions of the sexes, with no direct measurement of survival have largely been limited to male-biased sex ratios, in which higher male survival was inferred (Lloyd, 1973; Godley, 1964; Lloyd and Webb, 1977; Opler and Bawa, 1978; Webb and Lloyd, 1980). One case where female higher survival was invoked to explain a female-biased sex ratio (Melampy and Howe, 1977) has been questioned by others working on the same species in the same study site (Opler and Bawa, 1978), but the latter reference also reports cases where female plants appear to live longer than males in three other species. Thus, differential survival of the sexes may favor either males or females, and can result in a biased adult ratio in favor of whichever sex has the higher survival.

In Valeriana edulis the differential survival of the sexes may favor either sex, depending upon the population. In two populations of

V. edulis higher female survival (NRG, BI) apparently increased the female bias seen in the adult sex ratios, a result similar to that found for Rumex and Silene spp., above. In two other populations of V. edulis no differential mortality (BCR) or apparently higher male survival (BCP), was found. The latter phenomenon elevated the proportion of males in this population compared to the average sex ratio for the species. From the sample of populations in this study it appears that for V. edulis the conditions under which male survival exceeds that of females is rarer than the reverse. To my knowledge, no other cases have been documented where each sex has an advantage in terms of survival rate under certain, differing conditions. There are strong implications of such a case in a study by Freeman et al. (1976) in which local sex ratios in four species ranged from male to female biased across a soil moisture gradient. Either differential survival or environmental sex determination could have produced this pattern. In V. edulis no evidence of the latter has been found. Although the particular environmental conditions for V. edulis which affect male or female differently could not be clearly defined in the present study, the relationship between sex ratio and factors such as altitude and population density in the four main populations are suggestive that environmental effects are involved. It is difficult to imagine a set of environmental conditions that would be expected to favor female survival over male survival. Given the lower male than female reproductive expenses characteristic of V. edulis, (Chapter 2), males should have all the advantages in terms of survival, and yet clearly, conditions under which they do not are not uncommon. Resolution of this difficulty lies in the discovery of costs or risks which are greater to males than females.

Sex Differences in Reproductive Maturity and Adult Sex Ratios

In *Valeriana edulis*, sex differences in size at first maturity were not a strong factor contributing to adult sex ratios in any of the four populations. Still, in three out of four populations, the estimated size at maturity was somewhat smaller for males than females. Males mature at earlier ages, or smaller sizes in a number of species (Clark and Orton, 1967; Opler and Bawa, 1978; Melampy and Howe, 1977; Godley, 1976). To my knowledge, the opposite phenomena, females maturing earlier than males, has not been found in plants. In some instances early male maturity was thought to contribute to male-dominated sex ratios in natural populations (Opler and Bawa, 1978; Melampy and Howe, 1977; Meagher, 1981a), but in others, no effect was found (Opler and Bawa, 1978). Several cases where differences in age at maturity for the sexes and differences in survival of the sexes affect the sex ratio in opposite directions were reported in Opler and Bawa (1978), but populations still exhibit biased sex ratios. In these cases the affect of survival was greater than the effect of maturity, similar to the results for *V. edulis* in this study.

All species with reported early male maturity are long-lived, iteroparous species. It may be that in such species the class of plants just reaching reproductive maturity often do not make up a large enough proportion of the population to have a profound effect on the sex ratio of the whole population. In *V. edulis*, the proportion of plants that were apparently in this class ("smallest flowering plants") ranged from a maximum of 20% in population BCP to about 17% in population NRG, to 13% in population BCR, to 9% in population BI. Even a very strong male-bias in less than 10% of the population, as seen in BI, would have little effect on the overall population sex ratio. Thus it is important to know not only the life history characteristics of each sex, but also the population structure to correctly interpret influences on the adult sex ratio.

Environmental Correlates with Sex Ratio

The comparisons of environmental and population characters which could potentially influence sex ratio were difficult to interpret in this study since trends appearing among the four study sites disappeared when six minor study sites were included. A few deserve comment because comparable data from other species is available. In the four main populations, the proportion of females increased with increasing altitude. In contrast, Grant and Mitton (1979) found a definite increase in the proportion of males as altitude increased in populations of aspen (*Populus tremuloides*). In this sample of populations of *V. edulis* altitude may not have been correlated with stress, as it often is; even though population BI was near the upper limits for this species in this region, this population had the highest average plant size of all populations sampled. In the four main populations of *V. edulis*, the proportion of males declined as the average plant size increased. Melampy and Howe (1977) working with the tropical tree, *Triplaris americana*, and Lloyd (1973) working with dioecious Umbelliferae found that the proportion of males increased as the mean plant size in a population increased. They both interpreted size in terms of age of plants in each population. Nevertheless, these results differed from those for *V. edulis*. Sex ratio in natural populations of Rumex acetosa and R. thyrsiflorus was not related to density (Zarzycki and Rychlewski, 1972), similar to the results for V. edulis. Freeman et al. (1976) found that sex ratio in four desert species were biased in favor of males in dry areas and females in wet areas. Again, this is a contrast to data for V. edulis where if anything, females were favored in drier areas.

The clearest message that comes out of this portion of this study is that in order to interpret the influence of environmental factors on a phenomenon such as sex ratio in long-lived plants, it is necessary to sample numerous populations, and to carefully define the relationship of each factor to the environmental requirements of the species. Only when it is clear what factors represent to the plants will it be possible to draw conclusions about the influence of certain factors on sex ratio, or to make meaningful comparisons with other species.

Female-Biased Sex Ratios Prior to Adulthood

The best indications obtained from the field study reported here are that the sex ratio of "sub-adults" just prior to the onset of reproductive maturity (the "initial" adult sex ratio) is usually about 38% males, a significant female-bias. Most other species with female-biased sex ratios have been annuals, or short-lived perennials (Lloyd, 1973), but at least one other long-lived species, Triplaris americana exhibits female-biased sex ratios (Melampy and Howe, 1977). The initial adult ratio averaging 38% in V. edulis may or may not be equal to the primary sex ratio depending upon whether or not males and females have equal survival during the juvenile period. At this point, I cannot determine which stage the sex ratio first becomes female-biased in V. edulis.

Examination of the literature provides few clues, as none of the cases of female-biased adult sex ratios have been completely explained. Female biased primary sex ratios occur following heavy pollination in three of the species exhibiting female-biased adult sex ratios (*Rumex acetosa* and *R. thyrsiflorus*, Rychlewski and Zarzycki, 1975, and Correns, 1928 referenced therein; *Silene alba*, Mulcahy, 1967 and Correns, 1928). However, the heavy pollination levels used in experimental studies of *Rumex acetosa* were much greater than found under natural pollination conditions (Zarzycki and Rychlewski, 1972). Natural pollination resulted in a 1:1 primary sex ratio, and thus could not explain the female-biased adult sex ratios found in natural populations (Zarzycki and Rychlewski, 1972). On the other hand, in some cases *Silene alba* produced a higher proportion of female offspring in natural populations under presumably "heavy pollination" (high proportion of male flowers present) than under "light pollination" (low proportion of male flowers) (Mulcahy, 1967). Unfortunately, this study did not include enough counts of progeny sex ratios to draw definite conclusions.

Nearly all species with female-biased adult sex ratios have heterogametic males (Lloyd, 1974), a condition also found in *Valeriana dioica*, another dioecious species in the same genus as *V. edulis*. Lloyd (1974) proposes that in such species, there is a female bias in the primary sex ratio caused by differential fertilization by male and female-determining ("X" and "Y") pollen due to genetic inefficiency of the Y chromosome. This argument can be regarded as a genetic explanation for the earlier hypothesis (Correns, 1928, referenced in

Lloyd, 1974) of differential rates of pollen tube growth by male and female-determining pollen. The earlier version explained female-biased sex ratios resulting from "heavy pollination" on the basis of competition between male and female-determining pollen types. Under light pollination little competition should occur and the primary sex ratio was expected to be about 1:1. Lloyd's version of this hypothesis predicts a female-bias even with light pollination. Lloyd's version also requires sex chromosomes, which have not been identified in Valeriana spp. to my knowledge. Nevertheless, following Correns' and Lloyd's hypotheses, one might expect V. edulis to show female-biased primary sex ratios, at least when pollination is heavy.

A weakness of Lloyd's proposal is that it supposes that the primary sex ratio is not actively selected, but is merely a consequence of the sex-determination system. This is countered by a long string of literature which has argued that the primary sex ratio is indeed adjusted by natural selection (Fisher, 1930; Shaw and Mohler, 1953; Kolman, 1960; MacArthur, 1965; Emlen, 1968a and b; Spieth, 1974), and arguments that the sex determination systems are selected to optimize the sex ratio (Shaw, 1958; Eshel, 1975). Further, it is not clear from Lloyd's treatment whether or not male heterogamety and female-biased adult sex ratios are actually correlated in dioecious plants, as he does not report the frequency of heterogamety among dioecious plants which do not have biased sex ratios.

The alternative explanation, that the primary sex ratio in V. edulis is not female-biased (i.e., 1:1) and that the adult female bias is caused by females having higher survival than males during juvenile stages, also finds little support in the meager literature. Rumex acetosa females apparently mature earlier and are generally larger and live longer than males, thereby resulting in a female-biased adult sex ratio (Zarzycki and Rychlewski, 1972; Putwain and Harper, 1972). However, it is not clear whether these sex differences occur during juvenile stages as well as in adulthood. Few instances for any dioecious species of any sex differences during the juvenile stages have ever been documented (Lloyd and Webb, 1977), but this may be partly due to the difficulty of knowing the sex of juveniles. Still, because juvenile plants have no sexual organs, it may seem unlikely for sexual differentiation to occur at this stage (Lloyd and Webb, 1977; Meagher, 1981a; but see Lloyd, 1973). However, if the juvenile period were as long as seven years in V. edulis (not unusual for a long-lived perennial; see Meagher and Antonovics, 1981), males would only need to have about 2% lower survival per year than females to achieve the overall average survivorship from seeds to adults observed in the field (see Chapter 4) and a sex ratio of 38% male upon sexual maturity. Although this is only a small difference in survival rate of the sexes per year, over the whole juvenile period it would amount to about a 40% difference.

A study of sex differences in mortality rates during juvenile stages is hampered by the difficulty of sexing plants prior to reproductive maturity (especially, dead plants!). This problem can be resolved by detailed cytogenetic work. If the primary sex ratio among seeds (embryos) can be obtained (an easier task than sexing dead seedlings, though still requiring cytological genetic analysis) the problem of sex differences in survival rate among juveniles can be solved by growing a cohort from seeds to maturity, recording survival, and observing the sex ratio upon sexual maturity. Similarly, if seedlings could be grown to maturity with 100% survival under experimental conditions, the sex ratio of seeds (primary sex ratio) would be known, and any differences in survival of juveniles under natural conditions could be determined by subtraction. This approach has been used by others with success (e.g. Meagher, 1981a), but takes patience in a long-lived species which may not flower for several years after germination.

If the primary sex ratio in *V. edulis* is female-biased, as I suspect, it is necessary to explain why, since primary sex ratios are generally expected to be 1:1 at equilibrium (Fisher, 1930; and others, see below). Fisher's argument for a 1:1 primary sex ratio is based on the simple observation that each offspring has exactly one male and one female parent. Thus, the total reproductive contribution of all males is equal to that of all females. It follows that if one sex is in the minority, individuals of that sex have a higher average contribution to the next generation, and should therefore be produced in greater numbers. By this means selection will tend to stabilize the primary sex ratio to 1:1. Cases where primary sex ratios are not 1:1 require special circumstances, and are of interest because they reveal the constraints on the more common case of a 1:1 sex ratio. Factors which can result in a biased primary sex ratio are:

1) differences in parental investment per offspring for male vs. female young (Fisher, 1930; Kolman, 1960; Bodmer and Edwards, 1960); 2) inbreeding (Hamilton, 1967; Maynard Smith and Stenseth, 1978); 3) apomixis, or other asexual reproduction (Opler and Bawa, 1978); 4) differential survival and age of maturity in repeat-breeders with

overlapping generations (Emlen, 1968a,b); 5) gamete selection prior to fertilization (Lloyd, 1974; Correns, 1928); 6) some sex determination systems (Westergaard, 1958; Ross, 1978); 7) group selection (e.g., Lewis, 1942; Mulcahy, 1967; Kaplan, 1972; Eshel, 1975; Colwell, 1981; Wilson and Colwell, 1981).

Several of these are probably not appropriate to V. edulis. Number 1) is probably of little or no consequence in plants, since parental investment consists only of seed maturation, and to date no differences in seed size of males vs. females has been found (Gross and Soule, 1981). Number 2) seems unlikely to be of great importance in V. edulis since seeds are equipped with a pappus for wind dispersal, pollination is by insects capable of long distance pollen dispersal, and populations are fairly large. One would expect a fair amount of outbreeding in this situation. Regarding Number 3), field bagging trials showed no evidence of apomixis in V. edulis (Soule, unpublished), and there are no reports of apomixis or disparate chromosome numbers (sometimes indicative of apomixis) in the genus to my knowledge. There is no vegetative or other form of asexual propagation. Number 4), differential survival and maturity, deserves more time below. Number 5), gamete selection, discussed above, is questionable in Lloyd's form, but apparently has validity in the form of gamete competition. It is possible that such an effect occurs in V. edulis, and experiments involving different pollination levels would be illuminating.

Number 6), sex determination system, may have some application here. Ross (1978) proposed a genetic model of sex determination which facilitated the evolution of subdioecy from gynodioecy. Since there are gynodioecious species in the genus *Valeriana*, this is a likely course for evolution of dioecy in *Valeriana edulis*. *V. edulis* has a slight degree of male-inconstancy, in which rare males produce a few viable seeds. The female-fertile flowers on the males are of several forms (personal observation), a situation which coincides nicely with Ross's model wherein at subdioecy, there are several essentially "male" genotypes present. However, Ross's model predicts male-biased sex ratios, whereas in *V. edulis* we find female-biased sex ratios. Breeding experiments with the various types of males found in *V. edulis* would be required to determine the importance of this factor in creating a biased primary sex ratio.

Returning now to Number 4), this is a rather controversial point in the literature. Most theoretical treatments of selection for the primary sex ratio have concluded that differential survival of the sexes *cannot* influence the equilibrium primary sex ratio (e.g. Fisher, 1930; Shaw and Mohler, 1953; Kolman, 1960). These treatments have dealt with simple, discrete generation, single reproductive episode models, and their conclusions are correspondingly simplified. Emlen (1968a and b) comes to the opposite conclusion. The difference seems to be that only Emlen (although first suggested by MacArthur, 1965) incorporated any age structure into his model. Emlen allowed his model population to breed more than once per lifetime, and to have age-specific survival and fecundity. This creates a situation where the reproductive value (or contribution to "r") of male and female offspring must be used when considering selection of the sex ratio. With these considerations, both differential survival and age of maturity of the sexes influence the optimal primary sex ratio. I believe that Emlen is more nearly correct in this case, inasmuch as reproductive value is correlated with fitness (this assumption has recently been questioned; Caswell, 1980), although his work has received virtually no recognition. Because *V. edulis* does exhibit differential survival and maturity of the sexes, and is a long-lived repeat-breeder, it seems very likely that these components of reproductive value have influenced the equilibrium value of the primary sex ratio in this species. A stage transition population dynamics model for *V. edulis* (developed in Chapter 4) could be modified and used to investigate the influence of sex differences in survival and maturity on the optimal primary sex ratio for this species.

Finally, addressing number 7), many authors have invoked group selection to explain female-biased adult sex ratios in plants (e.g., Lewis, 1942; Mulcahy, 1967; Kaplan, 1972), relying on the explanation that female-biased sex ratios produce higher seed set in the population. Although this argument appears to be valid in organisms with certain population structures (small, isolated subgroups, or demes; Colwell, 1981; Wilson and Colwell, 1981), *V. edulis* does not appear to qualify. With attributes such as long life, wind-dispersal propagules and fairly large population size, *V. edulis* (along with many other species) probably has a high rate of gene-mixing occurring every breeding cycle.

In summary, it appears that in *Valeriana edulis* when a cohort of plants reaches maturity, the sex ratio is already female-biased. This is an unusual case, in that this species is a long-lived, iteroparous species, whereas other species with female-biased adult sex ratios are mostly annuals. Differences in survival of the sexes and population structure combine to either lessen or increase the bias of adult sex ratios in this species. It is possible that the primary sex ratio of *V. edulis* is also female-biased. This could be caused by the influence of differences in survival or age of maturity between the sexes on the equilibrium value of the primary sex ratio, or by a complex system of sex determination, or by gamete competition. It is also possible that juvenile survival rates of the sexes differ enough to account for the female biased sex ratio seen upon sexual maturity. The approach of documenting the life history characteristics of males and females in several populations in concert with the demographic characteristics has proven to be a valuable tool in understanding the adult sex ratio in *Valeriana edulis*.

CHAPTER 4

A POPULATION DYNAMICS MODEL FOR THE DIOECIOUS PLANT, *VALERIANA EDULIS* NUTT.

INTRODUCTION

In recent years attention among plant ecologists has turned towards the dynamics of plant populations. Investigation and description of plants population dynamics and life history characteristics which contribute to these dynamics can be an important step in understanding several levels of problems. For example, at the autecological level, such an investigation increases understanding of how species adapt to their environments. At a community level, this knowledge can contribute to understanding of a species' position in a community, whether it is a permanent or transient member, for instance.

Population dynamics are influenced by birth and death rates of the various classes of individuals composing the population. It has been demonstrated repeatedly that size is often a better predictor of fate than age in plants (Hartshorn, 1975; Werner, 1975; Sohn and Policansky, 1977; Gross, 1980; Meagher and Antonovics, 1981). An effective way of modelling the dynamics of a population that is size- or stage-structured is a matrix projection model (Lefkovitch, 1965), a variation of Leslie's age-structured projection model. Lefkovitch (1965) showed that any subclassification of a population should yield the same population growth rate, so that size or age are equally valid subclassifications. This type of model has been used successfully to characterize the dynamics of plant populations several times (Hartshorn, 1975; Sarukhan and Gadgil, 1974; Sohn and Policansky, 1977; Werner and Caswell, 1977), and to investigate the sensitivity of population growth rate to changes in various life history features (Hartshorn, 1975; Caswell and Werner, 1978). All of the above dealt with hermaphroditic plants and so contained only one classification with respect to sex.

In a dioecious plant population two sorts of subclassifications are of importance: size, or maturity classes, and sexes. It has been found that in dioecious plants, birth and death rates, and growth rates often differ for the sexes (see Lloyd and Webb, 1977 for review of this literature; Meagher and Antonovics, 1981). Recently, Meagher (1981b) used a projection matrix approach to model the dynamics of an iteroparous dioecious plant, Chamaelirium luteum. His model includes classifications based on sex and stage or size. In this paper I report on a model of population dynamics in Valeriana edulis, also an iteroparous dioecious plant. This model is similar to Meagher's in that it is subclassified by sex and stage or size, but it is a simpler model, and serves a somewhat different purpose than Meagher's. Meagher obtained population growth rates, equilibrium population structure, and reproductive value of each sex. The model presented here yields population growth rates and equilibrium population structure, but also investigates the sensitivity of population growth rate and population structure (particularly adult sex ratio) to a) the primary sex ratio (sex ratio among seeds), and b) differential survival of the sexes.

The primary sex ratio is not known for V. edulis, and the model provides a way of exploring the consequences of different primary sex ratios. It is of special interest to explore the consequences of sexual differences in life history traits on population dynamics in dioecious plants, where such differences are thought to increase male fitness (relative to other males), or female fitness (relative to other females). It is not clear that the results of selection among males or among females will always result in a set of population characteristics with the most "favorable" population dynamics (see Chapter 1 and 2). The model presented here is too simple in that males are not assigned any reproductive output (seed production), to allow direct calculation of male and female reproductive value. Modifications to assign reproduction to males are discussed which would allow this step to be made at some future time. I do calculate average number of seeds present per male and per female (called "parentage" subsequently) at equilibrium.

METHODS

Description of the Model

A simple size class and stage projection matrix model was developed from field data for each of four populations of *Valeriana edulis*, in order to determine population growth rates, stable size distribution, and equilibrium adult sex ratio. In these matrices, M, each element M(i,j) represents the probability that an individual of size (or stage) i at time t will move to size (or stage) j at time t+1. Individuals were classified into stages or size classes (adults): SEEDS, SEEDLINGS, JUVENILES, and ADULTS size 1, size 2, size 3, size 4 (size 4 occurred in 3 of the 4 populations). Adults were defined as all plants with more than 10 leaves, or plants with less than 10 leaves and flowering. Adult size classes were chosen by a method proposed by Vandermeer (1978) designed for size-based projection matrix models to minimize errors of sample size and distribution in choosing size classes (see Soule, 1981b). This was performed for each population separately, so size classes are not identical in the four populations.

Plants in each size/stage class were also classified by sex. Thus, each class was represented twice in the matrix - once for males and once for females. A(1,j) refers to male seeds and A(2,j) refers to female seeds. Similarly, A(3,j) refers to male seedlings, and A(4,j) to female seedlings, and so forth. The probability of a male seed at time t becoming a male seedling at time t+1 lies in element A(1,3), and, because plants do not change sex, elements A(1,2) and A(1,4), etc. are empty. Obviously, at least half of the elements of this matrix are empty, i.e., all those elements which pair odd and even subscripts. Elements that lie below the diagonal in this matrix are transitions to more advanced stages, or larger sizes. Elements on the diagonal are probabilities of remaining in the same stage or size class from t to t+1, and elements above the diagonal represent transitions backward, or shrinkage. Shrinkage only happens among adult size classes, as seedlings cannot become seeds, etc. The first two rows of the matrices represent the "birth rate", in this case, seed production, and are calculated as the number of births (seeds) per individual of each reproducing size class. Seeds containing male embryos are in row 1, A(i,1) and female seeds are in row 2, A(i,2).

The largest eigenvalue of such a matrix represents the finite rate of population growth, $\lambda_m = e^r$, at equilibrium (Lefkovitch, 1965). The eigenvector corresponding to λ_m gives the stable size structure of the population at equilibrium (applicable as long as $\lambda \geq 1.0$; $\lambda < 1.0$ is a declining population, not expected to achieve a stable size structure (Werner and Caswell 1977).

Parameter Estimation

Adult size class transition probabilities were obtained from direct field observations of more than 600 marked individuals followed for three seasons in each population (Soule, 1981b). Thus, size transitions were obtained for plants from yr 1 to yr 2, and for plants from yr 2 to yr 3 (including some newly marked in yr 2). Size was measured as cm diameter at the crown-leaf intersection. The average growth increment was highly variable among individuals, populations, and especially from year to year.

To determine how year to year variation might affect population growth rates, two transition matrices were constructed for each population. One was meant to set a maximum growth rate bound, and the other was meant to represent the average growth rate during this study. (Note that the average during this study is probably close to a minimum rate, since the lowest growth rates observed were negative. Thus, this "average" matrix is probably closer to a "minimum" bound.) To set the maximum bound in each population, the sample in each size class (yr 1 - yr 2, or yr 2 - yr 3, or yr 1 - yr 3) with the highest average individual growth increment was selected and that data used to calculate the transition probabilities for plants in that size range. These matrices are referred to as MAX GR series. The average matrix was taken from the pooled data from yr 1 - yr 2, and yr 2 -yr 3, for each population. These are referred to as MEAN GR series. Both MAX GR and MEAN GR matrices use the same field-observed survival rates, seed-juvenile transitions, and size-specific fecundity. Individual growth increments were lower in all but one case (population BCR females) in data used to form MEAN GR than in MAX GR (Table 4-1).

To obtain the probability of surviving and of changing classes at time t+1, transition rates in the MAX GR and MEAN GR series were multiplied by size-, and sex-specific survival rates, also obtained from the field from marked individuals (Table 4-2). In population NRG, which had exceptionally high survival, no deaths were recorded in the largest size class, so an arbitrary survival rate slightly less than 1.0 was set. These matrices are in Tables 4-3 and 4-4 respectively.

In three of the populations, male survival rates were different from female rates (one significantly so, see Chapter 3). To test the effect of this sexual difference on population growth another series of matrices was prepared. These used the same size-transitions as MAX GR, but were multiplied by a constant (equal) survival rate for males and females, and are referred to as the MAX GR/EQ l_x series (Table 4-5). Survival rates used were the average of the male and female rates for each size class, in three populations (BCR, NRG, BI); in the fourth population (BCP), the female survival rates were used, in order to observe the effect of changing the average survival rate in addition to equalizing male and female survival.

The juvenile class was defined by observing the size of new recruits in yr 3 on grids where all plants were marked in yr 2 (in populations BCR, NRG, and BI). It was found that new recruits nearly always had no more than 10 leaves. Further, marked plants with 10

Table 4-1. Average annual plant growth increments calculated from data used to construct transition matrices, MAX GR and MEAN GR, for *Valeriana edulis*.

		change in diameter, cm	
		MATRIX SERIES	
POPULATION		MAX GROWTH	MEAN GROWTH
BCP	male	1.71	0.58
	female	0.95	0.54
BCR	male	0.66	-0.53
	female	0.69	0.78
NRG	male	1.63	0.52
	female	2.27	0.81
BI	male	1.59	0.63
	female	0.57	-0.04

Table 4-2. Survival rates used in transition matrices for population dynamics model of *Valeriana edulis*. Plant size indicates range of adult size category.

		MAX GR and MEAN GR		MAX GR/EQ l_x
POPULATION	PLANT SIZE, cm	MALE	FEMALE	MALE and FEMALE
BCP	1 - 4 cm	0.9240	0.7575	0.7500
	5 - 7	0.9208	0.7525	"
	8 - 21	0.9152	0.7400	"
BCR	1 - 4	0.9589	0.9612	0.9657
	5 - 8	0.9704	0.9722	"
	9 - 14	0.9606	0.9713	"
	15 - 28	0.9586	0.9634	"
NRG	1 - 6	0.9622	0.9920	0.9745
	7 - 10	0.9710	0.9934	"
	11 - 22	0.9714	0.9941	"
	23 - 38	0.9677	0.9933	"
BI	1 - 6	0.9361	0.9817	0.9665
	7 - 9	0.9445	0.9858	"
	10 - 14	0.9544	0.9887	"
	15 - 36	0.9270	0.9797	"

Table 4-3. Adult transition probabilities for MAX GR series matrices.

			MALES					FEMALES		
	STATUS		STATUS YR 1			STATUS		STATUS YR 1		
POPULATION	YR 2	A7	A9	A11	A13	YR 2	A8	A10	A12	A14
BCP	A7	0.5544	0.0657	0.1017		A8	0.4418	0.0442	0.0336	
	A9	0.2772	0.4604	0.2034		A10	0.1894	0.4426	0.1009	
	A11	0.0924	0.3947	0.6102		A12	0.1263	0.2656	0.6055	
BCR	A7	0.6974	0.1941	-	-	A8	0.5607	-	-	-
	A9	0.1743	0.5175	0.3232	0.0798	A10	0.4005	0.8974	0.1079	-
	A11	0.0872	0.1941	0.5656	0.3195	A12	-	0.0748	0.6476	-
	A13	-	0.0647	0.0808	0.5592	A14	-	-	0.2158	0.9634
NRG	A7	0.6123	0.1386	-	-	A8	0.6617	0.0748	-	-
	A9	0.3498	0.5548	-	-	A10	0.3303	0.4486	-	-
	A11	-	0.2774	0.7065	0.2104	A12	-	0.3738	0.6631	0.1659
	A13	-	-	0.2649	0.7573	A14	-	-	0.3310	0.8274
BI	A7	0.7489	-	-	-	A8	0.6749	0.3148	-	-
	A9	-	0.7084	0.0531	-	A10	0.3068	0.3148	0.2081	-
	A11	0.0936	0.1967	0.7953	0.1545	A12	-	0.2361	0.7286	0.2062
	A13	0.0936	0.0394	0.1060	0.7725	A14	-	0.0787	0.0520	0.7735

Table 4-4. Adult transition probabilities for MEAN GR series matrices.

			MALES					FEMALES		
			STATUS YR 1					STATUS YR 1		
POPULATION	STATUS YR 2	A7	A9	A11	A13	STATUS YR 1	A8	A10	A12	A14
BCP	A7	0.6160	0.1381	0.1376		A8	0.6542	0.0579	0.0218	
	A9	0.2464	0.5064	0.2890		A10	0.0688	0.5788	0.0870	
	A11	0.0616	0.2762	0.5298		A12	0.0344	0.1157	0.6311	
BCR	A7	0.7732	0.1998	0.0346	0.1667	A8	0.7153	0.1157	0.1079	0.1968
	A9	0.1237	0.5137	0.2424	0.0417	A10	0.2459	0.7870	0.2158	-
	A11	0.0618	0.0856	0.5194	0.2084	A12	-	0.0694	0.4316	-
	A13	-	0.0285	0.1732	0.5418	A14	-	-	0.2158	0.7707
NRG	A7	0.8683	0.0607	-	-	A8	0.8246	0.1212	-	-
	A9	0.0939	0.5462	-	-	A10	0.1546	0.6299	0.1221	-
	A11	-	0.3541	0.8905	0.2104	A12	0.0129	0.2423	0.6453	0.1727
	A13	-	-	0.0809	0.7573	A14	-	-	0.2268	0.8206
BI	A7	0.7549	0.0394	0.0265	0.0281	A8	0.8134	0.3286	0.0593	0.0192
	A9	0.0604	0.4329	0.1060	0.0281	A10	0.1683	0.3834	0.1384	0.0576
	A11	0.0906	0.3936	0.5567	0.2528	A12	-	0.2464	0.6130	0.1537
	A13	0.0301	0.0787	0.2651	0.6180	A14	-	0.0274	0.1780	0.7492

Table 4-5. Adult transition probabilities for MAX GR/EQ l_x series matrices.

		MALES					FEMALES			
		STATUS YR 1					STATUS YR 1			
POPULATION	STATUS YR 2	A7	A9	A11	A13	STATUS YR 1	A8	A10	A12	A14
BCP	A7	0.4525	0.0538	0.0838		A8	0.4399	0.0433	0.0342	
	A9	0.2262	0.3770	0.1676		A10	0.1885	0.4435	0.1028	
	A11	0.0754	0.3232	0.5028		A12	0.1257	0.2661	0.6170	
BCR	A7	0.7024	0.1931	-	-	A8	0.5633	-	-	-
	A9	0.1756	0.5150	0.3219	0.0804	A10	0.4024	0.8140	0.1073	-
	A11	0.0878	0.1931	0.5633	0.3219	A12	-	0.0743	0.6438	-
	A13	-	0.0644	0.0804	0.5633	A14	-	-	0.2146	0.9657
NRG	A7	0.6202	0.1392	-	-	A8	0.6500	0.0750	-	-
	A9	0.3543	0.5568	-	-	A10	0.3245	0.4502	-	-
	A11	-	0.2784	0.7088	0.2118	A12	-	0.3752	0.6500	0.1627
	A13	-	-	0.2657	0.7626	A14	-	-	0.3245	0.8118
BI	A7	0.7732	-	-	-	A8	0.6645	0.3221	-	-
	A9	-	0.7249	0.0537	-	A10	0.3020	0.3221	0.2034	-
	A11	0.0866	0.2013	0.8054	0.1611	A12	-	0.2416	0.7121	0.2034
	A13	0.0966	0.0403	0.1074	0.8054	A14	-	0.0805	0.0508	0.7630

leaves or fewer rarely flowered. Thus, for populations BCR, NRG and BI, records from marked plants with not more than 10 leaves were used to determine probabilities of surviving, and either passing into the adult class (either growing to more than 10 leaves, or flowering qualified as a transition into the smallest adult class), or remaining in the juvenile class. In population BCP, where no grid was established, plants up to 2 cm diameter with no record of flowering were classified as juveniles and used to calculate juvenile transition probabilities. The transition probabilities and survivorship of juveniles was equal for both male and female categories. (Juvenile survival could be manipulated in future analysis of the model to see the effect on population structure of differences between males and females in pre-reproductive survival.)

Seed input per size class was calculated from the number of seeds per female inflorescence (averaged across all plant sizes, from direct field counts) multiplied by the average number of inflorescences per female plant for each size class, times the probability of flowering for females of each size class. This yields the number of seeds produced per female averaged over both flowering and vegetative females for each adult size class. These seeds were then divided into male-producing and female-producing seeds according to the given primary sex ratio for each particular run of the model. For example, for a primary sex ratio of 35% male, 0.35 x number of seeds was attributed to each adult female column in row 1 (male seeds), and 0.65 of the seeds went into row 2 (female seeds). Thus seed input was in positions A(1,8), A(1,10)... and A(2,8), A(2,10)... etc.

At this stage of the model, males have not been assigned any seed production, so reproductive value of males and females cannot be evaluated separately (as was done by Meagher, 1981b). In future analysis of this model, it would be illuminating to assign one-half of all the seeds produced to males (since males contribute one-half of the genes of the offspring). The problem in doing this is that total seed production is based on the number of females present, not on the number of males (assuming that pollen does not limit seed production). To calculate the number of seeds per male, it is necessary to first know total seed output, which requires knowledge of the number of females present. Then, half the total seeds can be assigned to males and this number divided by the number of males present, weighted by size specific abundance of males, and in this the size-specific seed output of males is obtained. Obviously, this can only be calculated after equilibrium has been established. Meagher (1981b) used this method of assigning seeds to males, and pointed out that if the adult sex ratio deviates from the primary sex ratio, then the average male seed contribution could not have been constant throughout the establishment of equilibrium, and this after-the-fact calculation cannot be accurate. Meagher (1981b) attempted to resolve this problem by using a "stabilizing" process in which he adjusted male seed contribution after equilibrium, and then obtained a new equilibrium, continuing this process until population growth rate stabilized. It is not entirely clear that even this method yields an accurate estimate of reproductive value. For the present model only the equilibrium seed output of males is known, by calculation from the stable size distribution at equilibrium. In the future it would be desirable to link male and female matrices in such a way that male seed output could be calculated with continual adjustments for changing adult sex ratio.

The transition from seedlings to juveniles was obtained in populations BCR, NRG and BI from the grids of marked plants. The number of recruits (new juveniles appearing on grids each year, i.e., 1 yr old plants) per m^2 divided by the number of seedlings (or seeds in the case of BI, see below) per m^2 equals the transition probability. The same transition probability was used for male and female seedling categories because it is not possible to identify sex in the vegetative stage. Number of seedlings per m^2 was calculated from the number of females/m^2 and the number of seedlings/female.

The transition probability from seeds to seedlings was determined from the percentage of seeds germinating in petri dish trials. For BI, no seeds were collected, so this transition was given a probability of 1.0, and the transition from seeds to juveniles (from observed recruitment) substituted for the transition from seedlings to juveniles (see above).

Primary sex ratios (hereafter, 1°SR) of 35% male and 50% male were used for all three matrix series and all four populations.

RESULTS

Population growth rates (λ) of 1.00 or greater occurred only in populations NRG and BI (Table 4-6), but in most cases λ's were only very slightly less than 1.0, indicating that most populations are near a stable population size. Both MAX GR and MEAN GR matrices produced $\lambda > 1.0$ for NRG, with 1°SR of either 0.35 or 0.50. A 1°SR of 0.65 in MEAN GR caused λ to drop below 1.0. In population BI, MEAN GR, with 1°SR = 0.35 gave the only value of $\lambda > 1.0$ for this population. The

Table 4-6. Population growth rates, λ_m, from a population dynamics model for four populations of *Valeriana edulis*. Primary sex ratio = proportion of males.

MATRIX SERIES	PRIMARY SEX RATIO	POPULATION BCP	 BCR	 NRG	 BI
MAX GR	0.35	0.9188	0.9884	1.0023	0.9970
	0.50	0.9188	0.9844	1.0004	0.9926
MEAN GR	0.35	0.9328	0.9749	1.0021	1.0016
	0.50	0.9328	0.9734	1.0002	0.9979
	0.65		0.9719	0.9983	0.9939
MAX GR/EQ. l_x	0.35	0.7963	0.9881	0.9842	0.9889
	0.50	0.7886	0.9843	0.9820	0.9843

highest λ achieved in population BCR was also with MAX GR and a 1°SR = 0.35. The highest λ for population BCP only, 0.9328, occurred in MEAN GR.

In all cases a 1°SR of 0.35 gave λ's higher than (or equal to in population BCP) the λ's obtained with a 1°SR of 0.50. This is the expected result since only females produce seeds in this model. The more females, the higher the population growth rate.

To examine the effect of the differential survival of males and females on λ, the population growth rates for matrix series MAX GR/EQ l_x are compared to those for MAX GR. The results are straight forward. For populations BCR, NRG, and BI, matrix MAX GR/EQ l_x in which male and female survival were set equal at the average rate, gave somewhat lower λ's than MAX GR (Table 4-6). This result is due to the fact that female survival from field records was somewhat higher than male in these populations, and so the average survival was therefore slightly lower than the female survival used in MAX GR (see Table 4-2). As in the 1°SR comparison, it is apparent that as the proportion of females increases, so does λ. In population BCR, where male and female survival are very close, the λ's calculated using MAX GR/EQ l_x and MAX GR are also very close. In population BCP where both male and female survival were set equal to female survival, the growth rate, λ, was again lower for MAX GR/EQ l_x than for MAX GR. Here male survival rather than female was reduced in MAX GR/EQ l_x , because male survival was higher than female in this population. Thus, although female survival has more effect on λ than does male, (λ rose in populations NRG and BI when female survival increased, even though male survival declined and the male-female average remained constant), male survival does also influence λ. This is shown by the fact that in population BCP λ decreased when male survival decreased even though female survival remained constant.

Between populations, apparently the best predictor of λ is female survival rate. Female survival was highest in NRG, second in BI, third in BCR and lowest in BCP (Table 4-2). This order corresponds to the order of magnitudes of λ's regardless of 1°SR (Table 4-6) for both MAX GR and MEAN GR where these natural survival rates were used. It also holds true in MAX GR/EQ l_x where average survival was used, since average survival rates ranked in the same order as female rates (Table 4-2).

Recruitment, as indicated by the ratio of juveniles to adults in equilibrium populations, did not appear to be correlated with λ among populations (Table 4-7). Population NRG, with the highest λ in MAX GR and MEAN GR, had only about one-fourth as many juveniles proportionately as population BCR (MAX GR) or population BI (MEAN GR). Within populations, however, recruitment seemed to be correlated with λ. For example, in BCR at 1°SR = 0.5, both the lowest juvenile to adult ratio and the lowest λ occurred in MEAN GR (Tables 4-3 and 4-2).

The matrices in series MAX GR and MEAN GR were designed to put boundaries on population behavior depending on whether over the long term individual plant growth rates are closer to the maximum rates observed or closer to the average rate observed. Both series use the same survival rates and juvenile dynamics because only one estimate of each of these was obtained from field data. The population structure (ratio of juveniles to males to females) at equilibrium predicted from these two models (from the eigenvectors corresponding to λ_{max}) differ

Table 4-7. Ratio of juveniles to adults at predicted equilibrium for four populations of Valeriana edulis. (Primary sex ratio = 0.50)

MATRIX SERIES	POPULATION BCP	BCR	NRG	BI
MAX GR	-	0.0680	0.0172	0.0170
MEAN GR	-	0.0356	0.0140	0.0580
MAX GR/EQ 1_x	0.0954	0.0688	0.0102	0.0468

somewhat from the observed structures. By comparing the observed population structure from field samples to the predicted equilibrium structure it is possible to discern whether or not the populations are currently at equilibrium, and which matrix seems to fit best (Table 4-8). Population structure is not shown for population BCP because of low λ_m, indicating that it is a declining population which will eventually go extinct, rather than attaining a stable population structure. All other populations with $\lambda < 1.0$ had λ's close enough to 1.0 that slight fluctuations in various parameters could presumably shift λ to > 1.0, and thus, their eigenvectors are probably close to equilibrium population structure.

In all cases for populations BCR, NRG, and BI more juveniles were observed in the field than are expected at equilibrium, suggesting that these populations may still be in an expanding phase. For BCR, the observed structure was closest to the equilibrium structure in MAX GR, 1°SR = 0.35 (Table 4-8). At equilibrium this model predicts a somewhat greater proportion of females than was observed. In population NRG, the observed population structure is closest to the equilibrium predicted by MAX GR, 1°SR = 0.5 (Table 4-8), but again the predicted equilibrium structure is more female-biased than that seen in the field. In BI the observed values are closest to the equilibrium structure predicted by MEAN GR, 1°SR = 0.35 (Table 4-8), and once again, the predicted structure is somewhat more female-biased.

Several alternatives may explain the greater female bias in the predicted equilibrium structure than in observed population structure in these populations. This difference might be resolved simply by the 1°SR actually being a bit higher than was used in the model. A strong

Table 4-8. Comparison of predicted equilibrium population structure with field observations in three populations of *Valeriana edulis*. a) MAX GR series; b) MEAN GR series.

		PERCENT OF POPULATION			
		1°SR = 0.35		1°SR = 0.50	
POPULATION		EQUILIBRIUM	OBSERVED	EQUILIBRIUM	OBSERVED
a) BCR	juvenile	7.6	21	6.4	21
	male	31.5	30	46.2	30
	female	60.9	49	47.4	49
NRG	juvenile	1.8	12	1.7	12
	male	14.6	28	20.8	28
	female	83.7	61	77.5	61
BI	juvenile	6.9	17	1.7	17
	male	15.3	24	20.8	24
	female	77.8	59	78.5	59
b) BCR	juvenile	3.5	21	3.4	21
	male	7.4	30	10.7	30
	female	89.1	49	85.9	49
NRG	juvenile	1.4	12	1.4	12
	male	12.0	28	17.3	28
	female	86.6	61	81.3	61
BI	juvenile	9.4	17	4.8	17
	male	20.2	24	31.2	24
	female	70.4	59	63.9	59

alternative is that juvenile survival of the sexes may actually differ, and the discrepancy between observed and expected population structures may be due to the equal juvenile survival rate used for males and females in the model. A biased primary sex ratio (as used in the model) might be a poor substitute for unequal juvenile survival. A third possibility is that the populations are actually still expanding, and not at equilibrium. Survivorship differences accumulate in older plants, having the most dramatic effects among oldest plants and in populations with a high proportion of older plants. Thus if female bias is largely caused by higher female than male survival (either in juvenile or adult stages), then populations still in an expanding phase (with a greater proportion of young plants) should have a less female-biased sex ratio than would be predicted at equilibrium. However, since calculated population growth rates were so close to 1.0, indicating nearly stationary population size, this alternative is perhaps less satisfying than others. Future analysis of the model, which will determine the effect of unequal rates of juvenile survival for males and females, may help to resolve this discrepancy between observed and predicted population structure.

At the equilibria predicted in these models, the average number of seeds parented by the typical male plant of V. edulis is greater than the average female seed parentage (Table 4-9). Average parentage can be looked at in two ways: seeds parented per flowering individual (based on expressed sex ratio, see Chapter 3), which is a measure of the relative contribution of each sex per cohort of seeds; or, seeds parented per individual whether flowering or vegetative (based on basic sex ratio, Chapter 3), which is a measure of the average annual

Table 4-9. Average number of seeds parented per male and per female, from equilibrium population structure in three populations of Valeriana edulis. a) Average annual seed output = number of seeds per adult male or adult female (flowering or vegetative) b) seed output/flowering episode = number of seeds per flowering male, or flowering female.

			MAX GR		MEAN GR	
POPULATION		1°SR	#/MALE	#/FEMALE	#/MALE	#/FEMALE
BCR	a)	0.35	1445	762	2756	229
		0.50	830	808	1854	230
	b)	0.35	2621	1246	5597	460
		0.50	1467	1306	3762	462
NRG	a)	0.35	9718	1692	9778	1350
		0.50	6375	1708	6440	1375
	b)	0.35	10129	1841	5213	1783
		0.50	6626	1851	3824	2316
BI	a)	0.35	1860	366	969	278
		0.50	6375	1712	321	157
	b)	0.35	2290	545	1222	388
		0.50	7531	2099	430	232

contribution over the lifetime of the parents. The difference between the sexes in average number of seeds parented is greater when considering average annual parentage than when comparing parentage per flowering episode (Table 4-9). The reason for this is that males flower more often than females in these populations (Chapters 2 and 3) so that basic sex ratio is even more female-biased than expressed sex ratio. Any greater average male parentage per flowering episode is compounded when higher male annual flowering frequency is also included, and therefore male and female parentage are more similar per flowering episode than per year.

The best comparison of male to female parentage for each population comes from the particular matrix series and 1°SR which produced an equilibrium population structure closest to the observed structure (see above). From these comparisons, the ratio of average parentage per year in males to that in females ranges from 1.9 in population BCR (MAX GR, 0.35), to 3.7 in NRG (MAX GR, 0.5), to 3.5 in BI (MEAN GR, 0.35). Thus, at predicted equilibrium the averge male fathers between 2 and 4 times as many offspring as an average female mothers per year, and each cohort of seeds has on the average only 1/2 to 1/4 as many male gene contributors as female.

DISCUSSION

The life history characteristics of *Valeriana edulis* combine to create population dynamics characteristic of a species inhabiting a stable environment. The predicted equilibrium population growth rates, λ_m, for three of the four populations studied were close to 1.0, indicating stable population size. This is not surprising, since the montane to subalpine meadows, or "parks" inhabited by _V. edulis_, are apparently a long-lived feature, and are climax community types for this region of the Rocky Mountains. Other studies in which population growth rates of long-lived species were obtained have also found that λ_m was near 1.0, indicating stable populations (e.g. Hartshorn, 1975; Meagher, 1981b).

The fourth population, BCP, proved to be declining. BCP occupies a fenced area used annually for temporary holding of cattle (hence the name "Brush Creek Pasture"). In the seasons I have observed, not only have the cattle eaten and trampled _V. edulis_ plants (cows seem to find _V. edulis_ tasty), but the pasturing has occurred just at the time when seeds are beginning to mature, and probably significantly reduced the chance of seeds maturing. The other three populations receive much less severe livestock grazing. BCR ("R" for Range) has cattle pass through for a day or so in some years. Cattle only occasionally reach NRG, and sheep, which also selectively graze _V. edulis_, visit BI in some years (1 out of the 4 years I observed this population). It is interesting that NRG, apparently with the least grazing pressure of all the populations, had the highest population growth rates.

Even though predicted population growth rates for _Valeriana edulis_ indicate stable populations, there were indications that three of the populations might actually be in an expanding phase, rather than at equilibrium. Both higher proportions of juveniles and higher proportions of males observed in the field than predicted by the models, could be interpreted as indications that populations are still growing. A possible explanation for this is that the communities of which _V. edulis_ is a part are maintained in a state of flux by disturbance. Pocket gopher activity was heavy in all four populations. In a nearby population of *V. edulis* I recorded the proportion of ground surface disturbed by pocket gophers at the time of snow melt in the spring, and found that 48% of 94 randomly selected 1/2 x 1/2 m square plots contained some pocket gopher disturbance. Although this disturbance does not always kill perennial plants, it does damage some, and it does provide substrate on which numerous seedlings of several other species germinate. If pocket gopher activity fluctuates in intensity over a period of several years, this, combined with intermittant livestock grazing may cause *V. edulis* populations in this region to fluctuate between expanding, stable, and declining states. An expanding phase a few years prior to this study could explain the current disproportionate abundance of juveniles and males in these populations.

It is interesting to discover that for *Valeriana edulis* samples yielding the highest average plant growth increment do not always yield the highest population growth rate. This was also found for *Dipsacus sylvestris* by Werner and Caswell (1977). Werner and Caswell (1977) performed a correlation analysis on their data and showed that the correlation between population and individual growth rates in eight populations of *D. sylvestris* was exactly zero. For *V. edulis* no formal analysis has been performed, but lack of correlation is apparent by inspection. In two populations the matrix formed from data yielding average plant growth increments gave higher λ than the matrix formed from data yielding maximum plant growth increments. Similarly, the population with the lowest λ (BCP, Table 4-6) had the second highest growth increment of all the populations in MAX GR. Examination of transition probabilities in BI (Tables 4-3 and 4-4) reveals that plants have a higher probability of moving into the next class in most cases in MEAN GR than MAX GR. Individual plant growth rates, which might be considered as a coarse indicator of "population health" are not indicative of population growth, since the latter also takes into account which plants are growing, which are reproducing, in addition to the rates of reproduction, recruitment, and mortality.

The factor that was found to have the greatest influence on λ in these populations is female survival rate. This was true both within and among populations. Population NRG, with the highest survival rates, had the highest population growth rates. Within populations, the matrix with the higher female survival rate also produced the higher growth rate. Similarly, a higher proportion of females in the 1°SR gave consistently higher population growth rates. Since only females produce seeds in this model, it is obvious that females have a greater impact on population growth rate than males, so this result is hardly surprising. The negative impact of decreased female survival on population growth rate is great enough to counteract increased male survival when the survival rates of the sexes are equalized, even though the average rate is unchanged (MAX GR/EQ l_x compared to MAX GR for BCR, NRG, BI). However, a decrease in male survival with no increase in female survival does reduce population growth rates, as expected (same comparison for BCP).

Thus, the differential survival of the sexes in favor of females in some of the populations of this species increases population growth rate. If not opposed by counterselection at the individual level selection at the group level might be responsible for such a pattern.

It is realistic in terms of population dynamics to assign all seeds to females, since this is the actual situation in nature. However, it is unrealistic in terms of population genetics to assign all seeds to females, since on the whole, male genetic contribution is equal to female in each generation. Thus, a conflict arises if one wishes to compare the effect of sexual differences not only on the dynamics of a dioecious population, but also on fitness of males and females. To make the genetic contribution realistic, one can divide total seed production by two and assign one half to all the males, and the other half to all the females (as in Meagher, 1981b). This method represents the genetic contributions of the sexes fairly, but can result in absurd population dynamics. Such a population could reproduce even without any females present (of course mine can without any males!). The relationship of reproductive value of males and females to the fitness of each sex from a model such as Meagher's is not entirely clear. Further, reproductive value is not always correlated with fitness, particularly in organisms (such as V. edulis) in which fecundity is related to size (Caswell, 1980).

Literature on human demography contains several two-sex models which attempt to solve this "problem of the sexes" (e.g., Goodman, 1967; Mitra, 1976; Mitra, 1978; Das Gupta, 1972 and 1976). However these are based on a principle of accrediting male parents with male births and female parents with female births (Mitra, 1978). Since this is neither the way that genetic inheritance operates, nor the way that reproduction occurs, I cannot see that it can clarify questions of either population dynamics or individual fitness.

Still, this problem needs solution. Perhaps nowhere is it more clear that we need a medling of population dynamic and population genetic models than here, a simple case of sexual difference in survival rate. While higher female survival contributes to higher λ_m thereby increasing λ_m of the average genotype in the population, at the same time, the resultant female-biased adult sex ratio causes average parentage per male to be greater than average parentage per female. The important question is, whether or not male fitness is correspondingly higher than female also, or whether the survival differences cancel these out. Two features of V. edulis make this a particularly complex quesiton to answer. One is that males flower more frequently at smaller sizes (and throughout their life) than females (Chapters 2 and 3), which could significantly raise male fitness compared to female through a reduced generation time. The second is that there are indiciations of a female bias prior to maturity, so that differential survival of adults may not account for the female bias entirely. Unless male life expenctancy is considerably less than female, it would seem that a parent could increase its genetic contribution to the next generation by producing sons rather than daughters. In other words, the predicted equilibrium population structure dictated by the population dynamics in these populations does not appear to be at a genetic equilibrium for the primary sex ratio. This situation, where adult sex ratio may feed back to the primary sex ratio, appears to be unique to iteroparous species in which males and females differ in age of maturity or flowering frequency, and was first formalized by Emlen (1968a, b) (see discussion in Chapter 3).

However, any conclusion that the primary sex ratio is not currently at equilibrium cannot be drawn definitively without calculating the fitness of males compared to females. This will have to await development of a separate model for just this purpose. Clearly, it is important to discover the primary sex ratio in *V. edulis*. A challenging area for future work is the interaction of the numerical and genetic equlibria regarding the distribution of males and females.

CHAPTER 5

SUMMARY

Investigation of sexual differences in a dioecious perennial plant, *Valeriana edulis*, lent insight into interaction of life history features with breeding system in this species. Major results follow:

1. Males had lower reproductive effort per flowering episode, and per year than females.

2. Males flowered more frequently than females.

3. Males first became reproductively mature at smaller sizes than females.

4. Males and females did not differ in their average growth rate or survival rate across populations, and no trade-off between growth or survival and reproductive expense was detected.

5. Adult sex ratio in *V. edulis* is consistently female-biased, averaging 38% male.

6. Within populations, slight differences between the survival rate of males and females may raise or lower the proportion of males.

7. Populations of *V. edulis* consist largely of older plants and therefore early maturity of males compared to females has little effect on adult sex ratio.

8. Three of four *V. edulis* populations studied were near stable size.

9. Higher female than male survival raises the population growth rate.

10. At predicted equilibrium, an average male in a *V. edulis* population parents two to four times as many seeds per year as an average female.

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