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POPULATION GENETIC CONSEQUENCES OF SMALL POPULATION SIZE: Implications for Plant Conservation

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Abstract

Although the potential genetic risks associated with rare or endangered plants and small populations have been discussed previously, the practical role of population genetics in plant conservation remains unclear. Using theory and the available data, we examine the effects of genetic drift, inbreeding, and gene flow on genetic diversity and fitness in rare plants and small populations. We identify those circumstances that are likely to put these plant species and populations at genetic risk. Warning signs that populations may be vulnerable include changes in factors such as population size, degree of isolation, and fitness. When possible, we suggest potential management strategies.

INTRODUCTION

Because of the key role they play in earth's ecosystems, plants should have the highest priority in conservation efforts. In terms of numbers, plant species dominate lists of rare and endangered species. For example, 214 plant taxa comprise over 75% of all taxa listed by the California Department of Fish and Game as rare, threatened, or endangered. Because of the large number of endangered plant species worldwide (estimated at approximately 60,000; 88), the primary method for their conservation must be in situ protection and

management. Success of these efforts will depend on identifying and thwarting general risks to the protected populations.

For over a decade, much attention has focused on the potential genetic risks associated with small population size, particularly from inbreeding and genetic drift (e.g. 1, 32, 95), but also from gene flow (25, 106). Nevertheless, the practical role of population genetics in plant conservation remains unclear. The theoretical risks are often straightforward extensions of population genetics theory; but relevant data have been slow to appear and are sometimes conflicting. Furthermore, the relative importance of genetics in conservation efforts has been called into question by some scientists who suggest that ecological factors may be more important (e.g. 61).

Our review addresses the following question: "Under what circumstances does population genetics play an important role in plant conservation biology?" We operate under the assumption that fragmentation, habitat destruction, and environmental stresses such as pollution limit or reduce the size of plant populations. Therefore, we examine the theoretical consequences of isolation and gene flow that put small populations at risk, compare the predictions with the available data from small plant populations and from endangered plant species, and discuss the present limitations of both theory and data. In each section, those general conditions in which plant species will be at genetic risk as well as the potential management strategies for protection are described. Our review focuses specifically on endangered plant species *in situ*. Space prevents us from reviewing other topics that fall within the general scope of "plant conservation genetics," such as germplasm collection and management and the transfer of engineered genes from crops into natural populations.

With the large number of species at risk and the limited amount of time and resources available, biologically based, easily applied general rules must be developed and employed. Therefore, the time has come for evaluating the general principles upon which management strategies will be based. Below, we identify when and whether population genetics plays an important role in the security of endangered plant species. At times, population genetics will be an important consideration; often, it will not be. Therefore, this review should serve as a framework for action for both plant conservation managers and biologists.

GENETIC DRIFT AND INBREEDING IN SMALL, ENDANGERED PLANT POPULATIONS

Two genetic consequences of small population size are increased genetic drift and inbreeding. Genetic drift is the random change in allele frequency that occurs because gametes transmitted from one generation to the next carry only

a sample of the alleles present in the parental generation. In large populations, chance changes in allele frequency due to drift are generally small. In contrast, in small populations (e.g. < 100 individuals), allele frequencies may undergo large and unpredictable fluctuations due to drift (9, 31).

Inbreeding is the mating of related individuals (31, 35). In plants inbreeding commonly occurs in two ways: (i) through selfing and (ii) through biparental inbreeding. Selfing, the most extreme form of inbreeding, may be prevented in plants by self-incompatibility or by dioecy (9). Biparental inbreeding will most likely occur when populations are small or when they exhibit spatial genetic structure. Structure will often develop when gene dispersal via pollen and seed are spatially restricted (e.g. 108).

Genetic drift and inbreeding may influence small plant populations by changing patterns of genetic diversity and fitness. These effects and their implications for conservation are discussed in detail below.

Effects on Genetic Diversity

Genetic drift changes the distribution of genetic variation in two ways: (i) the decrease of variation within populations (loss of heterozygosity and eventual fixation of alleles), and (ii) the increase of differentiation among populations. Every finite population experiences genetic drift, but the effects become more pronounced as population size decreases (31, 38). Wright (120) predicted that drift will substantially alter the organization of genetic variation of populations when $1/4N_e$ is much greater than the mutation rate (μ) and the selection coefficient (s) where N_e is the effective population size.

Effective population size is the number of individuals in an ideal population that would have the same genetic response to random processes as a real population of size N (23, 120). This concept is important because most population genetic theory deals with ideal populations. To best apply the predictions of population genetics, estimates of effective population sizes in nature are necessary. The effective population size is often depressed below the census size by factors such as deviations from one-to-one sex ratios, overlapping generations, variation in progeny production, and fluctuations in population size (37, 63, 100). While effective population sizes in nature are often difficult to measure, the ratio N_e/N is often expected to fall between 0.25 and 1.0 (Nunney & Campbell, in preparation).

Populations with continually small effective population sizes will be especially susceptible to the loss and reorganization of variation by genetic drift. However, any population that undergoes occasional fluctuations to small population size may also suffer from loss of variation by chance. Such fluctuations include population bottlenecks or founder/colonization events. Although allelic variation is likely to decrease with marked drops in population size, heterozygosity often remains relatively unchanged as long as population

size rebounds rapidly (9, 35, 38). The population genetic consequences of bottlenecks and founder events are reviewed by Barrett & Kohn (9).

Inbreeding increases homozygosity within populations. Smaller populations generally should lose heterozygosity faster than larger populations because the rate of loss is approximately equal to $1/2N_e$ each generation. In populations with continuous inbreeding, the frequency of heterozygotes should approach zero (38, 120).

Patterns of variation observed in endangered plants are expected to reflect theoretical predictions if drift and inbreeding are important influences on their genetic structure. Several approaches have been taken to evaluate genetic diversity in rare or endemic plants. Hamrick & Godt (46) asked whether allozyme variation in 449 plant species varied with geographical range (endemic, narrow, regional, or widespread). They found, both at the species level and within populations, that endemics contain significantly less genetic diversity than widespread species as measured by the proportion of loci heterozygous per individual, proportion of polymorphic loci, and alleles per polymorphic locus. They suggested that widespread species may have a history of large, continuous populations, whereas endemics might consist of smaller and more ecologically limited populations historically susceptible to loss of variation by drift or bottlenecks. Interestingly, endemic species had the same levels of genetic differentiation among populations as do widespread species.

Karron (54, 57) compared genetic variation in 11 sets of geographically restricted species and widespread congeners. He found that restricted species generally, but not always, contain less genetic variation than their widespread congeners as measured by percentage of polymorphic loci and number of alleles per polymorphic locus.

The above studies did not directly evaluate any association between population size and genetic variation because both endemic and restricted species (*sensu* 54) may occur in small populations or may be locally abundant. Yet, population size per se may explain differences in levels of genetic variation between widespread and rare congeners. Crawford et al (22), comparing four species of *Robinsonia*, found that the total genetic diversity was highest in the two most common species that had the largest population sizes. The rare *R. thurifera*, characterized by populations of fewer than 10 individuals, contained only 20% of the diversity detected in the other two species. Sytsma & Schaal (105) found that one widespread and one endemic species in the *Lisianthus skinneri* complex were genetically depauperate compared to three other endemics characterized by larger population sizes and more outcrossed breeding systems.

The above studies compared rare species with widespread species. However, if genetic drift has been important in determining genetic structure, then

smaller populations within a species should contain less variation than larger populations, and they should also show higher levels of interpopulation differentiation. We have compiled data for 10 species that compared levels and distribution of genetic variation among populations of different sizes within rare or endemic plant species

In these species, associations between population size and genetic variation are consistent with the hypothesis that the effects of genetic drift vary with population size. In Table 1, the measures of genetic variation most often positively associated with population size were percentage polymorphism (P) and number of alleles per locus (A). In a few cases, gene diversity (H_e) was associated with population size. When population size and variation covaried, among-population variation tended to be relatively high, in accord with the second prediction of the drift hypothesis. In the three studies where genetic variation and population size were not related, historical factors may be more important than current population size in determining patterns of diversity (19, 79); that is, populations in these studies may not be in evolutionary equilibrium.

The studies in Table 1 involved levels of electrophoretically detectable variation. However, quantitative variation may respond differently to small population size than do other types of variation (63). We are aware of only three relevant studies. Ouborg et al (82) investigated the correlation between population size and phenotypic variation in two rare species, *Salvia pratensis* and *Scabiosa columbaria*. They found that small populations ($N \leq 90$) contained less phenotypic variation than large populations ($N \geq 200$). While they could not separate genetic and nongenetic sources of variation, their

Table 1 Summary of studies associating population size and genetic variation in plant species.

Species	Range of population size	Positive association? (with ^a)	G_{st} ^b	Reference
<i>Acacia anomala</i> (Chittering populations)	3–50	No	0.06	19
<i>Eucalyptus caesia</i>	7–580	Yes (P)	0.61	78
<i>Eucalyptus crucis</i>	4–300	Yes (P, A, H_e)	0.24	93
<i>Eucalyptus parvifolia</i>	20–1350	No	0.07	84
<i>Eucalyptus pendens</i>	27–3000	No	0.08	79
<i>Eucalyptus pulverulenta</i>	30–3000	Yes (P, A, H_e)	0.30	83
<i>Halocarpus bidwillii</i>	20–400,000	Yes (P, A, H_e)	0.04	13
<i>Salvia pratensis</i>	5–1500	Yes (P, A)	0.16	111
<i>Scabiosa columbaria</i>	14–100,000	Yes (P, A)	0.18	111
<i>Washingtonia filifera</i>	1–82	Yes (P)	0.02	72

^a P = percent polymorphic loci, A = number of alleles per locus, H_e = gene diversity.

^b We consider $G_{st} > 0.1$ to represent high among population variation.

analysis suggested that at least part of the observed phenotypic variation is genetically based. These data suggest that morphological characters respond to population size variation in a similar manner to allozyme loci (111), supporting the hypothesis that genetic drift has been important in determining levels of variation in these populations.

In contrast, R. Podolsky (personal communication) found population size (range 30 – >1000) was not correlated with broad-sense genetic variance (V_g) for six continuous traits in *Clarkia dudleyana*. In fact, larger populations tended to have less variation than small populations. Similarly, Widen & Andersson (119) found that a small population (average $N = 130$) of *Senecio integrifolius* contained significant additive genetic variation for more characters than a large (average $N = 1260$) population. Differences in spatial structure may have influenced the retention of genetic variation in this case. The small population consisted of a series of small, isolated patches while the large population had a more continuous distribution.

Retention of genetic variation can also be affected by seed, bulb, and tuber banks that buffer populations against dramatic changes in genetic composition (7, 33). Long-term genetic stability in *Stephanomeria exigua* ssp. *coronaria* (39) and *Linanthus parryae* (29) has been attributed to genetic variation in the seed bank. Genetic differences between young and old seed bank subpopulations have been documented in *Carex bigelowii* (113) and *Luzula parviflora* (12). Similarly, rootstocks of *Delphinium gypsophilum* and its hybrids may maintain genetic diversity in the population (69). To our knowledge, studies of maintenance of genetic variation by seed banks in rare species are lacking, although some rare or endemic species have the potential to form long-lived seed banks (e.g. 10, 15, 44). Thus, the impact of seed banks on conservation genetics remains unknown.

IMPLICATIONS FOR CONSERVATION Because the effects of genetic drift and inbreeding may be especially pronounced in populations of limited size, we investigated whether restricted population size is characteristic of rare and endangered plants in California. We obtained permission to use the California Department of Fish and Game's RAREFIND (17) computer database, a compilation of information on the distribution and ecology of sensitive plant taxa in California. Specific occurrences are listed for 743 taxa. For the purposes of our survey, we assumed that each occurrence constitutes a single population. For each occurrence report, we recorded the most recent specific information regarding the number of individuals present on the site. Census data were available for 1 to 35 occurrences of 559 taxa for a total of 2993 data points. We found it necessary to make certain assumptions when population sizes reported were vague. For example, estimates given as "approximately 100 were assumed to contain close to 100 individuals. The

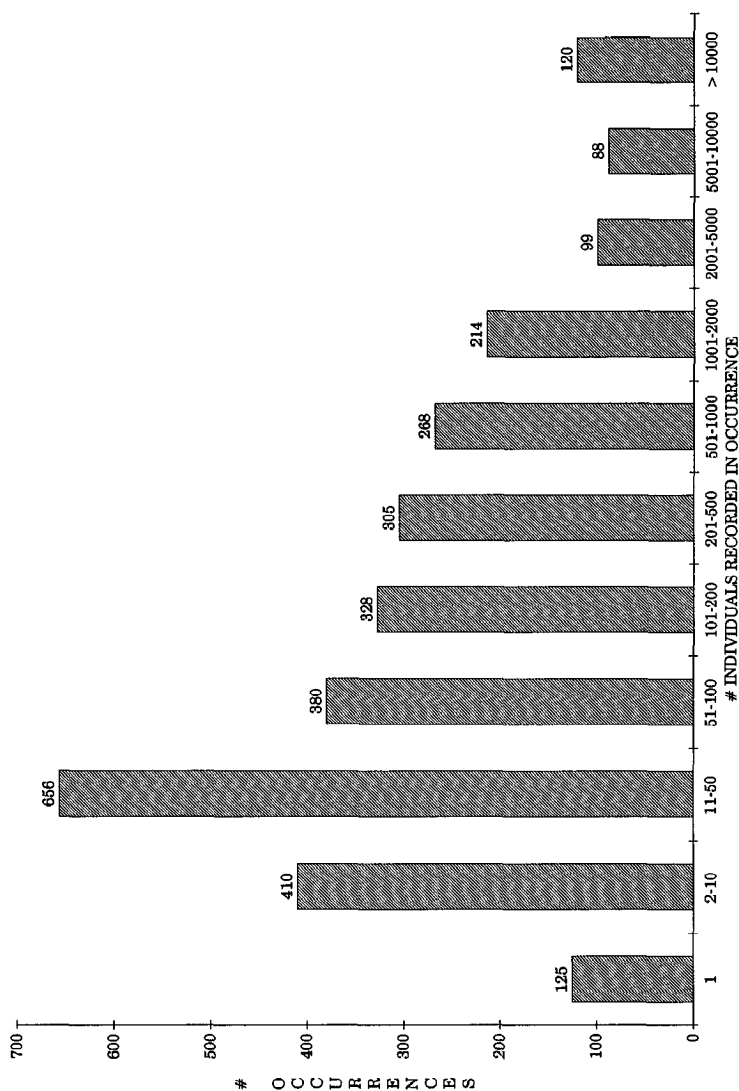


Figure 1 Number of individuals in occurrences of sensitive flora of California. (Each occurrence was assumed to constitute a single population. See text for more information.)

data are shown in Figure 1. Eighteen percent of the occurrences contained ten or fewer individuals, and 53% contained 100 or fewer individuals. These data suggest that sensitive plant taxa may regularly occur in small populations.

These data are apt to be biased toward small population sizes if biologists are more likely to report census numbers for small populations because they are easier to count than large populations. For example, vernal pool annuals, which are liable to occur in very large numbers, are rarely censused. Some occurrences were reported to contain "many" or "thousands" of individuals. This sort of information could not be used in our survey. Nevertheless, even if actual frequencies of small populations are half what we have estimated using RAREFIND, small populations of sensitive taxa (e.g. those with 100 or fewer individuals) are common enough that they, and genetic factors such as drift and inbreeding that influence them, would warrant specific study and attention by managers.

A drift-induced genetic change of concern is the erosion of genetic variation. Loss of genetic variation may decrease the potential for a species to persist in the face of abiotic and biotic environmental change (95, 100) as well as alter the ability of a population to cope with short-term challenges such as pathogens and herbivores (52).

Estimating levels of genetic variation in populations of concern should prove helpful for managers. The frequency of monitoring efforts will often be determined by practical considerations, such as staffing, funding, and the number of species of concern, but monitoring should be attempted approximately once per generation, if possible. With such monitoring, erosion of genetic variation could be rapidly recognized and steps taken to ameliorate losses. For example, introduction of migrants may slow or halt loss of genetic variation by drift (however, see below). Monitoring genetic variation could also provide information regarding the distribution of variation among populations. When a high proportion of genetic variation is distributed among, rather than within, populations, it is advisable to preserve more populations to ensure retention of allelic and genotypic diversity (e.g. 47).

When monitoring of genetic variation is feasible, it will likely involve the use of allozymes or PCR-based molecular markers. While such discrete markers have a number of advantages such as relatively low cost and nondestructive sampling, it is not clear how well their diversity is correlated with other types of diversity (e.g. 47). For example, consistent positive associations between morphometric and allozyme variation have not been found (45 and references therein). Such discrepancies may be important if different types of variation respond differently to small population size (63).

Because genetic data pertaining to the level and distribution of genetic variation will not always be available to managers, generalizations about the nature of genetic variation in small populations would be useful in making

management decisions. Though census population size is not necessarily a good predictor of current levels of genetic variation within populations, it should be a good indicator of what is liable to happen to genetic variation over time (i.e. how variation is expected to change as the population approaches evolutionary equilibrium) (112). The relationship between effective population size and current variation may be stronger than the relationship between census size and variation. If that is the case, then simple methods of accurately estimating effective population sizes should help managers to predict equilibrium levels of genetic variation. However, even without these data, erosion of genetic variation by drift should be minimal when populations are large. Therefore, other management considerations may take priority for large populations.

The history of a species may also provide some insight into contemporary patterns of genetic variation. When known, historical changes in population size and distribution should be considered by managers (47). Populations may be genetically depauperate if recent or recurrent fluctuations in population size (bottlenecks) have occurred. Changes in distribution and abundance are warning signs that genetic composition has changed or is liable to change.

Data concerning the presence and genetic structure of seed, bulb, and tuber banks, though rarely available, are also valuable in assessing vulnerability of populations to genetic erosion. These reserves of genetic variation may buffer populations against the loss of variation and help preserve the potential for adaptive changes (e.g. 44).

Effects On Fitness

Genetic drift and inbreeding influence fitness through inbreeding depression, the loss of fitness with increasing homozygosity. The precise mechanism by which increased homozygosity is related to decreases in viability and fecundity is controversial (18, 60).

The level of inbreeding depression may vary with the mating system. In typically inbreeding populations, the frequency of deleterious recessive alleles may decline as they become homozygous and are purged by selection (8). Thus, populations with a long history of inbreeding should be less vulnerable to inbreeding depression than typically outbreeding populations (18). However, in plants, the relationship between selfing rate and inbreeding depression is not precise, and some typically selfing species suffer from strong inbreeding depression (9). Theoretical work also suggests that the relationship between inbreeding depression and mating system may not be as straightforward as expected (50).

The extent of inbreeding depression may also be a function of population size. Inbred individuals in large populations with little spatial genetic structure or in populations that have recently become small are liable to exhibit

inbreeding depression as homozygosity increases. Chronically small populations may exhibit lower levels of inbreeding depression if deleterious recessive alleles have been purged by selection over time. On the other hand, small populations may suffer greater inbreeding depression than do larger ones because of the reduced effectiveness of selection relative to genetic drift (49); in small populations, deleterious recessives, rather than being eliminated by selection, could become fixed by chance.

Inbreeding depression has seldom been examined in sensitive plant species. Karron (56) compared geographically restricted and widespread *Astragalus* species and found no evidence of inbreeding depression in percent seed set and percent embryo abortion. He did, however, detect high levels of inbreeding depression for seedling biomass in progeny of the restricted species, *Astragalus linifolius*. This result is unexpected since frequent selfing in that species is expected to have purged the genome of deleterious recessive alleles (57).

We are aware of two studies relevant to the association between inbreeding depression and population size in sensitive plant species. Menges (74) found that germination percentage increased with population size in *Silene regia*. Large populations ($N > 150$) exhibited higher and less variable germination percentages than small populations, independent of region or isolation. Small populations may produce seeds of lower fitness because of inbreeding depression in recently reduced populations or inbreeding depression from increased selfing due to higher frequencies of intraplant pollinations. In contrast, the intensity of inbreeding depression measured in *Scabiosa columbaria* did not vary with population size (110).

Another area of relevant research involves the association between heterozygosity per se and fitness. Because some rare species are largely or fully monomorphic for the marker loci examined (e.g. 20, 66, 99, 115), it is of interest to ascertain whether heterozygosity per se is related to fecundity and viability. To our knowledge, the only relevant data for plants are for common species. Increased heterozygosity was associated with increasing age, earlier sexual maturity, and increased vegetative and reproductive output in *Liatris cylindracea* (94). In addition, heterozygosity and growth rate are positively correlated in some temperate tree species (64 and references therein; 77). Circumstantial evidence also comes from the observation that some predominantly inbreeding plants maintain higher levels of heterozygosity than expected (35 and references therein). Further, some studies have suggested that highly heterozygous organisms are better able to contend with fluctuating environments (52 and references therein).

On the other hand, *Pinus resinosa*, a widespread species, has very low levels of allozyme heterozygosity and is remarkably uniform morphologically (34). Two species of *Typha* also lack allozyme variation but exhibit consid-

erable ecological amplitude (71). These results suggest that heterozygosity is not requisite for ecological success (64).

IMPLICATIONS FOR CONSERVATION It appears difficult to predict when inbreeding depression will be an important factor decreasing the fecundity and viability of sensitive species. Selfing rates are not necessarily predictive of the expected level of inbreeding depression because even species with a long history of inbreeding may suffer from inbreeding depression (9). Currently, it appears that population size is also not necessarily a useful predictor of inbreeding depression, although more data are needed to clarify this relationship. In addition, the extent of inbreeding depression changes with the environment studied and may be more severe in competitive or otherwise challenging environments (e.g. 49, 110). If heterozygosity per se provides a significant fitness advantage, then population fitness might be estimated using levels of heterozygosity for discrete biochemical markers. Unfortunately, this approach may be risky because heterozygosity and inbreeding depression are not necessarily associated in a predictable way (49).

Because it is difficult to predict levels of inbreeding depression based on mating system, population size, and heterozygosity, monitoring fitness components in sensitive species may be the most reliable approach managers can take currently. Significant decreases in fruit or seed set, for example, suggest that intervention may be appropriate, although it will probably be unclear whether the reductions are caused by genetic factors. Ecological factors such as changes in pollinator fauna or behavior may be equally important in determining fitness in the short term (61, 101).

Changes in pollinator behavior in small or rare plant populations may decrease fitness if the frequency of intraplant (self) pollination increases, which may increase inbreeding depression (e.g. 74, but see 109), or if the overall visitation rate decreases. Significantly lower levels of pollinator visitation were observed in restricted *Astragalus linifolius* compared with widespread *A. lonchocarpus* (55). Lower visitation rates were associated with lower seed sets in *Dianthus deltoides* in fragmented sites compared to intact sites (53). These data suggest that an awareness of changes in the composition and/or behavior of the pollinator fauna may help managers detect fitness decreases in sensitive plant species.

Additionally, self-incompatible plants in small populations may suffer from problems finding a mate. In a simulation study, Byers & Meagher (16) found that small populations ($N < 50$) did not maintain a large diversity of self-incompatibility alleles. Therefore, the frequency of available mates decreased, and the variance of number of available mates increased. Thus, lower seed set per individual and increased variation in seed set among individuals were predicted in small populations. In this case, introduction of

individuals with different compatibility types might offset the observed changes. Although the compatibility genotype of individuals will almost never be known, knowing that a sensitive species is self-incompatible, dioecious, or otherwise obligately outcrossing may help managers recognize this cause of fitness decrease in diminishing populations (q.v. 65).

Managers may also wish to be especially conscious of species that have experienced recent reductions in population size relative to species that have a history of persistent small population size. The latter are apparently not immediately threatened by the lower average viability that may be associated with small population size (51 and references therein). Some chronically sparse prairie grasses presumably have a reproductive behavior that increases their likelihood of persistence despite low population size (86). Species in which recent changes in distribution, abundance, or fitness (e.g. fruit or seed set) are observed may be more immediately threatened than these historically rare species.

GENE FLOW IN SMALL, ENDANGERED PLANT POPULATIONS

Gene flow in plants is the successful movement of genes among populations by mating or by migration of seeds or vegetative propagules (26, 96). Many plant populations are geographically discrete. But geographic isolation may not ensure reproductive isolation, either within or among species (26). Therefore, gene flow may be relevant to the conservation genetics of a sensitive taxon in two situations: (i) when more than one population of the taxon is extant, and (ii) when opportunities exist for hybridization with related taxa.

Gene flow in plants is idiosyncratic, varying greatly among species, populations, and seasons. However, gene flow levels at isolation distances of hundreds to thousands of meters are frequently high enough to counteract genetic drift and moderate levels of directional selection (26). Even in predominantly self-fertilizing species, gene flow by pollen may occur at significant rates and substantial distances (114). Thus, gene flow cannot be ignored as a factor in plant conservation genetics. What levels of gene flow are expected for small plant populations?

Gene flow rate, the fraction of immigrants per generation, m , is expected to increase as recipient population size decreases, other things being equal. Two reasons are offered for this expectation: (i) As population size decreases, the relative fraction of a fixed number of immigrant pollen grains, seeds, and spores increases (48). (ii) For zoophilous species, optimally foraging pollinators spend more time within large populations than small populations, effecting proportionately more interpopulation matings in the latter (85).

Experiments with crops using a large source population and smaller sink populations have generally corroborated this expected relationship between population size and rate of gene flow by pollen (e.g. 11, 14, 21). In a few cases, data conflict with expectations. For example, Klinger et al (58) found a strong distance dependent trend. At short distance (1 m), theoretical expectations held; larger populations received less gene flow from a source population than did smaller populations. But at the greatest distance (400 m), the trend was reversed. No experiment has yet simulated the range of distances and population sizes found in natural populations. However, most experiments have shown that pollen gene flow rates generally increase with decreasing population size. We are not aware of data for the relationships of seed dispersal and source or target population size.

The size of the source population relative to sink population may be important in determining gene flow rate into the sink. Larger populations should export more pollen and seeds than small populations, creating a strong gene flow asymmetry from large into small populations. In an experimental study, Ellstrand et al (27) found essentially no gene exchange among three small populations (15 individuals each) of wild radish a few hundred meters apart, but substantial gene flow into them from very large populations (thousands of individuals) thousands of meters away. Again, we are not aware of any relevant data regarding seed dispersal patterns. In conclusion, small populations are expected to receive gene flow at a higher rate than large populations and are more likely to receive gene flow from large populations than from other small ones, even if the latter are in closer proximity.

Intraspecific Gene Flow

The role of intraspecific gene flow in plant conservation biology may be important if more than one conspecific population exists and if those conspecific populations are close enough for gene flow to occur (25). Despite the importance of gene flow and its prevalence in natural plant populations, studies of the genetics of sensitive plant species rarely address gene flow in the species of concern. Most tacitly assume that intraspecific gene flow rates are nil and that the populations under study are fully isolated.

Is this view well founded? We estimated the average levels of gene flow for 32 endangered or otherwise sensitive plant taxa (information available from authors), using the following formula for Nm (24), the average number of successful immigrants per generation:

$$Nm = \frac{1G_{st}-1}{4(n(n-1))^2}$$

where G_{st} is equivalent to a weighted average of Wright's (120) F_{st} over all alleles over all polymorphic loci (80) and n is the number of populations

sampled. This method is considered the most robust of those that use population genetic structure data to estimate gene flow (97). Although this estimate depends on the sampling scheme (see 26 for discussion), it is useful for judging the order of magnitude of gene flow. The Nm estimate from this method represents recent, rather than current, gene flow (97). For a sample of small populations ($N = \text{ca. } 10$), it reaches near-equilibrium in about 10 generations after a change in gene flow pattern (112). Therefore, it tends to overestimate gene flow for species with recently isolated populations.

Our analysis has certain limitations. It cannot be applied to species monomorphic at all loci studied (e.g. 66, 99). Furthermore, some of our estimates came from data on only one or two polymorphic loci. Thus, the values are crude. However, we found a wide range of gene flow for sensitive plant taxa with Nm estimates ranging from 0 to greater than 15; the distribution of values is typical for plants as a whole (40). The gene flow estimates are not associated with taxonomy, habit, breeding system, and pollination system. Estimates for ten *Eucalyptus* species ranged from 0.01 to 4.27. Furthermore, the three lowest gene flow estimates come from a highly selfing annual, an annual with an insect-pollinated mixed mating system, and an outcrossing, wind-pollinated tree.

EFFECTS ON GENETIC DIVERSITY AND FITNESS The best known evolutionary consequence of gene flow is that it works to homogenize population structure, acting against the effects of drift and diversifying selection (e.g. 62, 120). In the case of drift, the rule of thumb is that one immigrant every second generation or one interpopulation mating per generation ($Nm = 0.5$) will be sufficient to prevent strong differentiation (96). This result is independent of population size, but the time to evolutionary equilibrium depends on a variety of factors, including population size (112). Conservation geneticists often conclude that one migrant per generation will homogenize populations against the effects of drift (e.g. 1). Over half of the gene flow estimates we calculated for sensitive plant taxa are large enough to homogenize allele frequencies ($Nm > 0.5$; see above), suggesting gene flow has played an important role in organizing genetic diversity in these species.

The homogenization of genetic variation by gene flow is not necessarily the same as enhancement of local variation. Ultimate changes in local diversity will depend on the nature of genetic variation in the gene flow source populations relative to the sink populations. For example, the arrival of substantial gene flow from a genetically depauperate source will actually reduce the amount of variation in a relatively variable target population. As noted above, small populations are expected to have an asymmetric gene flow relationship with large populations. Such one-way gene flow will tend to make the small populations evolutionary "satellites" of nearby large populations.

Conservation geneticists have operated under the assumption that since migration increases effective population size, the same level of migration that maintains variation should prevent an increase in inbreeding depression in small populations (1). While this conclusion may be reasonable, to our knowledge the relationship between gene flow and inbreeding depression has never been addressed in theoretical detail (M. Slatkin, personal communication). The absence of research in this area may be due to the uncertainty of the genetic mechanisms underlying inbreeding depression (18). We predict that the impact of gene flow on inbreeding depression may also be a function of selective pressures on the populations involved.

If selection favors different alleles in different locations (disruptive selection), then gene flow of inappropriate alleles can prevent local adaptation and reduce local fitness (3, 118). In this case, the importance of gene flow increases as population size decreases. Generally, local adaptation cannot occur when $m > s$ where m is the fraction of immigrants per generation and s is the local selective coefficient against immigrant alleles (96). That is, moderate rates of gene flow (approximately 1–5% per generation) are sufficient to introduce genetic variation to counterbalance selection for local adaptation of the same magnitude (i.e. 1–5%). Available data support this expectation. Reciprocal transplant studies often show local adaptive differentiation in plant populations (reviewed by 68, 116, 117), but generally not at the microgeographic level at which substantial gene flow occurs (e.g. 5, 117) unless selection is very strong (e.g. 4; $s > 0.99$).

Most gene flow estimates we calculated for 32 sensitive plant taxa (see above) are probably too small to prevent adaptive differentiation under spatial disruptive selection. However, our largest estimates (two cases, $Nm > 10$) represent values that are large enough to oppose a disruptive selective coefficient of 0.2 in populations of 50 individuals.

Adaptive differentiation may lead to outbreeding depression, “a fitness reduction following hybridization” between populations (106). Outbreeding depression may be common in plants. Waser (116) reviewed 25 studies on the fitness effects of outcrossing distance in angiosperms and found evidence for outbreeding depression in nearly three quarters of the studies; the remainder showed fitness increases with increasing interparent distance. The fitness decline due to outbreeding depression can be substantial. In *Ipomopsis aggregata*, offspring from 100 meter matings were 32% less fit than progeny from 10 meter matings (118). Furthermore, in *Scleranthus annuus*, progeny from 75 to 100 meter matings suffered a 19 to 36% decrease in male fertility relative to those from 6 meter matings (104).

The frequency of outbreeding depression will be a function of population size if smaller populations receive gene flow at a higher rate than large populations. Problems may be exacerbated in small populations if gene flow

asymmetry leads to high rates of gene flow by pollen from large populations adapted to different conditions (3). Interestingly, either drift or gene flow can prevent local adaptation in small populations.

IMPLICATIONS FOR CONSERVATION Gene flow is usually considered beneficial in conservation biology, preventing inbreeding depression and depletion of genetic variation in small populations (e.g. 1, 52). But gene flow can also be detrimental for small populations because, under certain conditions, it can reduce local variation, prevent local adaptive differentiation, and reduce fitness through outbreeding depression. The role that intraspecific gene flow should play in *in situ* conservation management plans depends largely on the role it has played in recent evolutionary history of the species at risk. The primary concern occurs when gene flow has changed substantially; the general goal of plant conservation genetic management should be to maintain gene flow at levels that are roughly the same as historic levels.

How are plant conservation managers going to determine historic and current levels of gene flow? Order of magnitude historic levels of gene flow can be estimated from allele frequency data using the same formula we used to estimate Nm above (24). Because this estimator takes several generations to reach evolutionary equilibrium (97, 112), it should be a reasonable estimate of the historic levels of gene flow in many sensitive plant taxa prior to current conditions. For most perennials (and annuals with a long-term seed bank), it should give an adequate picture of gene flow over the last hundred years. The crude value obtained will suffice to assign the species at risk into the category of historically high or low gene flow.

Once species are assigned into such categories, determining whether gene flow has changed dramatically and in a direction to pose a new hazard will largely be a matter of common sense. For a taxon with historically high gene flow levels ($Nm > 0.5$), a sharp drop in gene flow due to habitat fragmentation or loss of pollinators may lead to problems that can be solved by gene flow augmentation. Former gene flow levels could be approximated by transplantation, by transport of seeds or spores, or by cross-pollination among populations. The transfer of a few successful genomes per generation per population will be sufficient to maintain gene flow at the historical order of magnitude. For most perennials, gene flow augmentation once every two decades would probably suffice. Furthermore, because species with histories of high gene flow have generally had little opportunity for differentiation, the geographic source of the immigration material will be largely irrelevant as long as the introduced material is not highly monomorphic or arriving from a distance great enough to cause outbreeding depression. No gene flow enhancement will be necessary for populations with historically high gene flow where gene flow levels have not changed

or increased; if gene flow is augmented, it would generally have no effect but would be a waste of effort.

For a taxon with historically low gene flow levels ($Nm < 0.5$), unchanged gene flow levels or increased isolation of the populations will have little effect on its population genetics. But if disturbance acts to increase gene flow for such a taxon, then gene flow may be deleterious because of the possibility of outbreeding depression. The impact of outbreeding depression varies with m , the fraction of immigrants introduced by gene flow. As population size decreases relative to a constant number of immigrants, the risk of outbreeding depression increases. Gene flow at the level of 1% or less will be of little concern; gene flow at rates of 10% or more may have a substantial impact on fitness. In such cases, management must include reducing gene flow. The specific solution will depend on why gene flow levels have increased.

Increased gene flow is most likely to arise in three situations: (i) if disturbance reduces the size of a population so that the fraction of seeds sired by immigrant pollen increases or the fraction of immigrant seed increases, (ii) if a common subspecies or race (particularly a weedy one) dramatically expands its range and becomes parapatric or sympatric with a rare subspecies or race, or (iii) if misguided conservation management efforts include transplantation to enhance gene flow or population size.

In the first case, reducing gene flow may be difficult. Management of pollinators or flowering times are potential solutions. Planting alternate hosts for the pollinators around the population may prove effective in intercepting immigrant pollen. Such "guard rows" or "barrier rows" are generally effective in preventing pollen from entering crop breeding blocks and seed production fields (see 36). Fortunately, the first case will probably be relatively rare.

In the second case, reducing gene flow requires a straightforward, if sometimes costly, solution—local eradication of the common relative of the taxon at risk. Eradication may be desirable also because the relative may be weedy enough to pose a competitive threat to the taxon at risk or other sensitive species in the region.

The third case is most likely and potentially most troublesome. Transplantation is often cited as a management solution to bring populations up to minimum viable size or to enhance local genetic diversity (references in 30). If the transplanted material comes from a population that has differentiated from the local population, the expression of outbreeding depression upon mating will be immediate and has the potential to be severe. Outbreeding depression is well-known as a problem in animal conservation genetics (106) and, in the case of reintroduced populations, "can be severe enough to increase chances of extinction greatly for a few generations" (95). Outbreeding depression created by conservation management has already caused the

extinction of an animal population (*Capra ibex ibex*, 107). Additionally, large transplantation projects often have other drawbacks (30). If evidence suggests that outbreeding depression will occur after transplantation, and if the number of transplants exceeds 10% of the current population size, the immediate problems accrued to the population would far outweigh the possible long-term benefits from increasing population size and/or genetic diversity. If no data are available, and transplantation is desirable, no more than a few transplants (no more than 1% of the extant population) would both minimize the impact of possible outbreeding depression and suffice to enhance genetic diversity.

The benefits and problems of gene flow should be addressed in any plant conservation management plan. Identification of most intraspecific gene flow problems or their amelioration should be straightforward. In most cases, recognition and consideration of gene flow as a potential hazard by plant conservation decision-makers will prevent future problems such as costly, unnecessary, and potentially problematic transplantation projects.

Interspecific Gene Flow

Interspecific gene flow occurs by hybridization and introgression (repeated backcrossing of a hybrid to one or both parental types—42). “Hybridization is a frequent and important component of plant evolution and speciation” (90). Perhaps more than 70% of plant species are descended from hybrids (42). Furthermore, natural interspecific and intergeneric hybridization are common in plants; well-studied examples number over 1000 (42, 102), and putative examples number in the tens of thousands (59).

The role of interspecific gene flow on plant conservation biology may be important when a population of a sensitive species and a population of partially or fully compatible relatives are close enough for substantial mating to occur (25). Despite the importance of hybridization and its prevalence in natural plant populations, reviews on plant conservation genetics rarely address interspecific gene flow (but see 89).

Is this neglect from the fact that interspecific gene flow in endangered species is so rare as to play an insignificant role in plant conservation genetics? To answer this question, we used the RAREFIND (17) database and others to identify California’s sensitive plant taxa with high potential for interspecific gene flow—those that are either hybridizing with more common taxa or are sympatric with congeners.

Removing situations of taxonomic ambiguity, we found 22 sensitive taxa (ca. 3%) involved in probable or documented hybridization with more common relatives (list available from authors). This list may be a significant underestimate of their numbers. Biologists submitting data on rare species might overlook hybridization. Also, conservation biologists might avoid mentioning hybridization because they recognize that sensitive species in-

volved in natural hybridization may fail to receive protection under strict interpretation of the "Hybrid Policy" of the US Endangered Species Act of 1973 (81).

As of late 1992, RAREFIND provided data on 743 (out of 1600+) sensitive plant taxa; 142 were locally sympatric with congeners. Therefore, interspecific mating is likely for over 19% of California's sensitive flora in the database, and hybrid swarms are known for about 3%. We also surveyed the 93 protected plant species of the British Isles (103) and found 9 (10%) that naturally hybridize with more common species. In California and the British Isles opportunities for interspecific gene flow are common enough to warrant consideration as a factor in plant conservation management. (For information on the conservation status of hybrids, see 81, 89.)

EFFECTS ON GENETIC DIVERSITY AND FITNESS Interspecific mating between a sensitive species and a common one will have one of two consequences relevant to conservation biology. If hybrid progeny and progeny from advanced hybridization are vigorous and fertile, then the species is at risk from genetic assimilation. If hybrid progeny are sterile or have reduced vigor, then the species is at risk from outbreeding depression.

Extinction from genetic assimilation occurs in the absence of selection against hybrids. The problem has been known in plants for decades. Ratcliffe (87) observed "species may be disappearing through introgression of a rare plant with a more common relative to produce hybrid swarms in which the characters of the rare species are finally swamped." Genetic assimilation has also been recognized as a conservation problem for many vertebrate species (e.g. 6, 76).

Small populations are at greater risk than large ones from genetic assimilation. As population size of the endangered species decreases relative to that of the sympatric congener, the effects of genetic assimilation become increasingly important. The situation also holds true for parapatric populations because of gene flow asymmetry discussed above.

Outbreeding depression is the other conservation problem associated with interspecific mating. Depending on the species involved, hybridization can drastically reduce a plant's maternal fitness. Decreased fitness can be manifest early as reduced seed set. The cost can be substantial. For example, crosses within species of *Gilia* subsection *Arachnion* result in few or no aborted seeds, but crosses among species typically result in seed abortion rates of 50% or more (41, 43). The dramatic fitness consequences of outbreeding depression may account for occasional reports of unusually low seed set when an endangered species is sympatric with a common relative (17).

Decreased fitness can also be manifest by the production of sterile or weak

hybrid progeny. For example, over 75% of the naturally occurring hybrids of the British Isles are fully or mostly sterile (102). Even if hybrid progeny are not sterile, if the parents are well-differentiated ecologically, their offspring might be able to grow and reproduce only in rare, intermediate microsites (2).

As in the case of intraspecific outbreeding depression, the frequency of outbreeding depression from interspecific mating is expected to increase as the size of the population in question decreases. Almost one out of five of California's sensitive flora have one or more populations sympatric with a congener. Many populations at risk have sizes smaller than 100 individuals (17) so that pollen flow from a sympatric relative could have a substantial impact on plant fecundity.

IMPLICATIONS FOR CONSERVATION Problems from interspecific gene flow will probably occur in only a fraction of the cases where a sensitive species is sympatric with a congener. Interspecific gene flow may be obvious by the presence of hybrids of intermediate morphology. If morphological traits are unreliable, hybridization may be confirmed by biochemical genetic methods (70, 91). If no hybrids are present, it should still be relatively easy to identify high risk situations.

First, species at risk must be sympatric with a congener for intermating to occur. While congeners could be native species, they could also be weeds, crops, or other domesticated plants (25). For example, a major threat to many endangered sunflower (*Helianthus*) species is hybridization with the weedy annual sunflower, *H. annuus*, which has dramatically expanded its range following human disturbance (92). Also, hybridization with domesticated species has been implicated in the extinction of at least six wild species (e.g. 98). In California, the rare *Juglans hindsii* is at risk of extinction by hybridization with cultivated walnut, *J. regia* (73).

Second, substantial intermating must occur. Intermating rates of 10% or more are probably sufficient to be detrimental. Pollen transfer rates can be crudely estimated based on knowledge of the distance between the congeners, their breeding systems, their phenologies, and their pollinators. Distance alone might be sufficient to keep the populations isolated. Generally, 50 m is sufficient to isolate a population if it is highly selfing (i.e. with typical outcrossing rates of < 10%) (28). But populations with high outcrossing rates (i.e. self-incompatible or dioecious species) require 500 m or more (28). Other types of prezygotic reproductive isolation are much more effective. For example, plants that flower in different seasons are highly isolated, as are those that do not share pollinators (67).

Even if pollen transfer occurs, intermating might not occur if the species are cross-incompatible (67). If pollen transfer is apparently substantial and

cross-compatibility is unknown, simple cross-pollination experiments should determine whether pollen tubes are arrested in the pistil (cross-incompatibility), fertilization occurs but a substantial fraction of seeds are aborted (outbreeding depression), or hybrids are produced (genetic assimilation).

Third, both the relative and absolute size of the population at risk will determine the impact of interspecific gene flow. High risk situations will occur when the congener is numerically superior to the vulnerable population. The difference may be functionally magnified if the congener population is reproductively more vigorous than the vulnerable population in terms of pollen production or pollen export (25). Also, when the vulnerable population becomes small enough for demographic stochasticity to become important (approximately 50 or less; 75), chance events may play a role in the relative frequency of interspecific mating.

If the evidence suggests a high risk of interspecific gene flow, then management steps must be swift and sure because of the speed at which genetic assimilation can occur and because of the substantial fitness losses accrued from outbreeding depression. Eradication of the gene flow source and/or transplantation are the only solutions for the problem (89). For example, Rieseberg et al (91) used isozymes to confirm hybridization in the world's only population of *Cercocarpus traskiae*. They suggested that a sympatric individual of *C. betuloides* be removed and that "cuttings representing the five 'pure' *C. traskiae* trees be transplanted to other areas ... where the risk of hybridization is minimal." In certain cases, it may also be necessary to eliminate all hybrid or introgressed individuals. That decision should be based on the ecological and genetic consequences of that action. In the case of *C. traskiae* above, removal of all hybrids would remove a substantial portion of the global population of the species and a substantial portion of its genetic variation (89).

SUMMARY

We have identified circumstances that put rare plant species and small populations at genetic risk. Although not all rare plants are at genetic risk, it will occur commonly enough to be of concern to conservation managers. Changes in factors such as population size, degree of isolation, and fitness are warning signs that populations may be vulnerable. Managers may be able to use pre-existing data to determine whether such changes have occurred, but additional experimental or descriptive evidence may be necessary to make a determination. When such data suggest that populations are likely to be at risk, mitigation measures may be straightforward and simple. We see our work as a first attempt to bring population genetic principles into a context for application by plant conservation managers.

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Literature Cited

1. Allendorf FW. 1983. Isolation, gene flow, and genetic differentiation among populations. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. CM Schonewald-Cox, SM Chambers, B MacBryde, WL Thomas, pp. 51-65. Menlo Park: Benjamin/Cummings. 722 pp.
2. Anderson E. 1948. Hybridization of the habitat. *Evolution* 2:1-9
3. Antonovics J. 1976. The nature of limits to natural selection. *Ann. Mo. Bot. Gard.* 63:224-47
4. Antonovics J, Bradshaw AD. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity* 25:349-62
5. Antonovics J, Ellstrand NC, Brandon RN. 1988. Genetic variation and environmental variation: expectations and experiments. In *Plant Evolutionary Biology: A Symposium Honoring G. Ledyard Stebbins*, ed. L Gottlieb, SK Jain, pp. 275-303. London: Chapman & Hall. 414 pp.
6. Baard EHW. 1989. The status of some rare and endangered endemic reptiles and amphibians of the southwestern Cape Province, South Africa. *Biol. Conserv.* 49:161-68
7. Baker HG. 1989. Some aspects of the natural history of seed banks. In *Ecology of Soil Seed Banks*, ed. MA Leck, VT Parker, RL Simpson, pp. 9-21. New York: Academic Press, Inc. 462 pp.
8. Barrett SCH, Charlesworth D. 1991. Effects of a change in the level of inbreeding on the genetic load. *Nature* 352:522-24
9. Barrett SCH, Kohn JR. 1991. Genetic and evolutionary consequences of small population size. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 3-30. New York: Oxford Univ. Press. 283 pp.
10. Baskin JM, Baskin CC. 1991. An eight-year greenhouse germination study of the cedar glade endemic *Onosmodium molle* subsp. *molle*. *Nat. Areas J.* 11:190-92
11. Bateman AJ. 1947. Contamination of seed crops. I. Insect pollination. *J. Genet.* 48:257-75
12. Bennington CC, McGraw JB, Vavrek MC. 1991. Ecological genetic variation in seed banks. II. Phenotypic and genetic differences between young and old subpopulations of *Luzula parviflora*. *J. Ecol.* 79:627-43
13. Billington HL. 1991. Effect of population size on genetic variation in a dioecious conifer. *Conserv. Biol.* 5: 115-19
14. Bond DA, Pope MD. 1974. Factors affecting the proportion of cross-bred and self-bred seed obtained from field bean (*Vicia faba*). *J. Agric. Sci.* 83: 343-51
15. Boyd RS, Serafini LL. 1992. Reproductive attrition in the rare chaparral shrub *Fremontodendron decumbens* Lloyd (Sterculiaceae). *Am. J. Bot.* 79: 1264-72
16. Byers DL, Meagher TR. 1992. Mate availability in small populations of plant species with homomorphic sporophytic self-incompatibility. *Heredity* 68:353-59
17. California Department of Fish and Game. 1992. RAREFIND. Natural Heritage Div./ Natural Diversity Data Base.
18. Charlesworth D, Charlesworth B. 1987. Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* 18:237-68
19. Coates DJ. 1988. Genetic diversity and

- population genetic structure in the rare chattering grass wattle, *Acacia anomala* Court. *Aust. J. Bot.* 36:273-86
20. Cole CT, Biesboer DD. 1992. Monomorphism, reduced gene flow, and cleistogamy in rare and common species of *Lespedeza* (Fabaceae). *Am. J. Bot.* 79:567-75
21. Crane MB, Mather K. 1943. The natural cross-pollination of crop plants with particular reference to the radish. *Ann. Appl. Biol.* 30:301-08
22. Crawford DJ, Stuessy TF, Haines DW, Cosner MB, Silva O, Lopez P. 1992. Allozyme diversity within and divergence among four species of *Robinsonia* (Asteraceae: Senecioneae), a genus endemic to the Juan Fernandez Islands, Chile. *Am. J. Bot.* 79:962-66
23. Crawford TJ. 1984. What is a population? In *Evolutionary Ecology*, ed. B Shorrocks, pp. 135-74. Oxford: Blackwell Scientific. 418 pp.
24. Crow JF, Aoki K. 1984. Group selection for a polygenic behavioral trait: estimating the degree of population subdivision. *Proc. Natl. Acad. Sci. USA* 81:6073-77
25. Ellstrand NC 1992. Gene flow by pollen: implications for plant conservation genetics. *Oikos* 63:77-86
26. Ellstrand NC 1992. Gene flow among seed plant populations. *New Forests* 6:241-56
27. Ellstrand NC, Devlin B, Marshall DL. 1989. Gene flow by pollen into small populations: data from experimental and natural stands of wild radish. *Proc. Natl. Acad. Sci. USA* 86:9044-47
28. Ellstrand NC, Hoffman CA. 1990. Hybridization as an avenue of escape for engineered genes. *BioScience* 40:438-42
29. Epling C, Lewis H, Ball FM. 1960. The breeding group and seed storage: a study in population dynamics. *Evolution* 14:238-55
30. Fahselt D. 1988. The dangers of transplantation as a conservation technique. *Nat. Areas J.* 8:238-44
31. Falconer DS. 1989. *Introduction to Quantitative Genetics*. New York: Wiley. 438 pp.
32. Falk DA, Holsinger KE, eds. 1991. *Genetics and Conservation of Rare Plants*. New York: Oxford Univ. Press. 283 pp.
33. Fiedler PL. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). *J. Ecol.* 75:977-95
34. Fowler DP, Morris RW. 1977. Genetic diversity in red pine: evidence for low genetic heterogeneity. *Can. J. For. Res.* 7:343-47
35. Frankel OH, Soule ME. 1981. *Conservation and Evolution*. New York: Cambridge Univ. Press. 327 pp.
36. Frankel R, Galun E. 1977. *Pollination Mechanisms, Reproduction, and Plant Breeding*. New York: Springer-Verlag. 281 pp.
37. Franklin IR. 1980. Evolutionary change in small populations. In *Conservation Biology: An Evolutionary-Ecological Perspective*, ed. ME Soule, BA Wilcox, pp. 135-49. Sunderland, Mass: Sinauer. 345 pp.
38. Futuyma DJ. 1986. *Evolutionary Biology*. Sunderland, Mass: Sinauer. 600 pp.
39. Gottlieb LD. 1974. Genetic stability in a peripheral isolate of *Stephanomeria exigua* ssp. *coronaria* that fluctuates in population size. *Genetics* 76:551-56
40. Govindaraju DR. 1988. Relationship between dispersal ability and levels of gene flow in plants. *Oikos* 52:31-35
41. Grant V. 1964. Genetic and taxonomic studies in Gilia. XII. Fertility relationships of the polyploid cobwebby gilias. *Aliso* 5:479-507
42. Grant V. 1981. *Plant Speciation*. New York: Columbia Univ. Press. 563 pp. 2nd ed.
43. Grant V, Grant A. 1960. Genetic and taxonomic studies in Gilia. XI. Fertility relationships of the diploid cobwebby gilias. *Aliso* 4:435-81
44. Griggs FT, Jain SK. 1983. Conservation of vernal pool plants in California, II. Population biology of a rare and unique grass genus *Orcuttia*. *Biol. Conserv.* 27:171-93
45. Hamrick JL. 1989. Isozymes and the analysis of genetic structure in plant populations. In *Isozymes in Plant Biology*, ed. DE Soltis, PS Soltis, pp. 87-105. Portland: Dioscorides. 268 pp.
46. Hamrick JL, Godt MJW. 1990. Allozyme diversity in plant species. In *Plant Population Genetics, Breeding and Genetic Resources*, ed. AHD Brown, MT Clegg, AL Kahler, BS Weir, pp. 43-63. Sunderland, Mass: Sinauer. 449 pp.
47. Hamrick JL, Godt MJW, Murawski DA, Loveless MD. 1991. Correlations between species traits and allozyme diversity: implications for conservation biology. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 75-86. New York: Oxford. 283 pp.
48. Handel SN. 1983. Pollination ecology, plant population structure, and gene

- flow. In *Pollination Biology*, ed. L. Real, pp. 163–211. Orlando: Academic Press. 338 pp.
49. Hedrick PW, Miller PS. 1992. Conservation genetics: techniques and fundamentals. *Ecol. Appl.* 2:30–46
50. Holsinger KE. 1988. Inbreeding depression doesn't matter: the genetic basis of mating system evolution. *Evolution* 42:1235–44
51. Holsinger KE, Gottlieb LD. 1991. Conservation of rare and endangered plants: principles and prospects. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 195–208. New York: Oxford. pp. 283.
52. Huenneke LF. 1991. Ecological implications of variation in plant populations. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 31–44. New York: Oxford Univ. Press. 283 pp.
53. Jennersten O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conserv. Biol.* 2:359–66
54. Karron JD. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evol. Ecol.* 1:47–58
55. Karron JD. 1987. The pollination ecology of co-occurring geographically restricted and widespread species of *Astragalus* (Fabaceae). *Biol. Conserv.* 39:179–93
56. Karron JD. 1989. Breeding systems and levels of inbreeding depression in geographically restricted and widespread species of *Astragalus* (Fabaceae). *Am. J. Bot.* 76:331–40
57. Karron JD. 1991. Patterns of genetic variation and breeding systems in rare plant species. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 87–98. New York: Oxford. 283 pp.
58. Klinger T, Arriola PE, Ellstrand NC. 1992. Crop-weed hybridization in radish (*Raphanus sativus* L.): effects of distance and population size. *Am. J. Bot.* 79:1431–35
59. Knobloch IW. 1972. Intergeneric hybridization in flowering plants. *Taxon* 21:97–103
60. Lacy RC. 1992. The effects of inbreeding on isolated populations: are minimum viable population sizes predictable? In *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management*, ed. PL Fiedler, SK Jain, pp. 277–96. New York: Chapman & Hall. 507 pp.
61. Lande R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–60
62. Lande R. 1992. Neutral theory of quantitative genetic variance in an island model with local extinction and colonization. *Evolution* 46:381–89
63. Lande R, Barrowclough GF. 1987. Effective population size, genetic variation, and their use in population management. In *Viable Populations for Conservation*, ed. ME Soulé, pp. 87–123. New York: Cambridge Univ. Press. 189 pp.
64. Ledig FT. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. ME Soulé, pp. 77–104. Sunderland, Mass: Sinauer. 584 pp.
65. Les DH, Reinartz JA, Esselman EJ. 1991. Genetic consequences of rarity in *Aster furcatus* (Asteraceae), a threatened, self-incompatible plant. *Evolution* 45:1641–50
66. Lesica P, Leary RF, Allendorf FW, Hilderback DE. 1988. Lack of genic diversity within and among populations of an endangered plant, *Howellia aquatilis*. *Conserv. Biol.* 2:275–82
67. Levin DA. 1978. The origin of isolating mechanisms in flowering plants. *Evol. Biol.* 11:185–317
68. Levin DA. 1984. Immigration in plants: an exercise in the subjunctive. In *Perspectives on Plant Population Ecology*, ed. R Dirzo, J Sarukhan, pp. 242–60. Sunderland, Mass: Sinauer. 487 pp.
69. Lewis H, Epling C. 1959. *Delphinium gypsophilum*, a diploid species of hybrid origin. *Evolution* 13:511–25
70. Liston A, Rieseberg LH, Mistretta O. 1990. Ribosomal DNA evidence for hybridization between island endemic species of *Lotus*. *Biochem. Syst. Ecol.* 18:239–44
71. Mashburn SJ, Sharitz RR, Smith MH. 1978. Genetic variation among *Typha* populations of the southeastern United States. *Evolution* 32:681–85
72. McClenaghan LR, Beauchamp AC. 1986. Low genic differentiation among isolated populations of the California fan palm (*Washingtonia filifera*). *Evolution* 40:315–22
73. McGranahan GH, Hansen J, Shaw DV. 1988. Inter- and intraspecific variation in California black walnuts. *J. Am. Soc. Hort. Sci.* 113:760–65
74. Menges ES. 1991. Seed germination percentage increases with population

- size in a fragmented prairie species. *Conserv. Biol.* 5:158-64
75. Menges ES. 1991. The application of minimum viable population theory to plants. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE, Holsinger, pp. 45-61. New York: Oxford Univ. Press. 283 pp.
76. Miller RR, Williams JD, Williams JE. 1989. Extinction of North American fishes during the past century. *Fisheries* 14:22-38
77. Mitton JB, Grant MC. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Annu. Rev. Ecol. Syst.* 15: 479-99
78. Moran GF, Hopper SD. 1983. Genetic diversity and the insular population structure of the rare granite rock species, *Eucalyptus caesia* Benth. *Aust. J. Bot.* 31:161-72
79. Moran GF, Hopper SD. 1987. Conservation of the genetic resources of rare and widespread eucalypts in remnant vegetation. In *Nature Conservation: The Role of Remnants of Native Vegetation*, ed. DA Saunders, GW Arnold, AA Burbridge, AJM Hopkins, pp. 151-62. Chipping Norton: Surrey, Beatty and Sons. 410 pp.
80. Nei M. 1973. Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. USA* 70:3321-23
81. O'Brien SJ, Mayr E. 1991. Bureaucratic mischief: recognizing species and subspecies. *Science* 251:1187-88
82. Ouborg NJ, van Treuren R, van Damme JMM. 1991. The significance of genetic erosion in the process of extinction II. Morphological variation and fitness components in populations of varying size of *Salvia pratensis* L. and *Scabiosa columbaria* L. *Oecologia* 86:359-67
83. Peters GM, Lonie JS, Moran GF. 1990. The breeding system, genetic diversity, and pollen sterility in *Eucalyptus pulverulenta*, a rare species with small disjunct populations. *Aust. J. Bot.* 38:559-70
84. Prober SM, Tompkins C, Moran GG, Bell JC. 1990. The conservation genetics of *Eucalyptus paliformis* L. Johnson et Blaxell and *E. parviflora* Cambage, two rare species from south-eastern Australia. *Aust. J. Bot.* 38:79-95
85. Pyke GH. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15:523-75
86. Rabinowitz D, Rapp JK, Cairns S, Mayer M. 1989. The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. *Am. Nat.* 134:525-44
87. Ratcliffe DA. 1973. Safeguarding wild plants. In *Plants—Wild and Cultivated: A Conference on Horticulture and Field Botany*, ed. PS Green, pp. 18-24. Hampton: Bot. Soc. of the British Isles. 231 pp.
88. Raven PH. 1987. The scope of the plant conservation problem world-wide. In *Botanic Gardens and the World Conservation Strategy*, ed. D Bramwell, O Hamann, V Heywood, H Synge, pp. 19-29. London: Academic Press. 367 pp.
89. Rieseberg LH. 1991. Hybridization in rare plants: insights from case studies in *Cercocarpus* and *Helianthus*. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE, Holsinger, pp. 171-181. New York: Oxford Univ. Press. 283 pp.
90. Rieseberg LH, Ellstrand NC. 1993. What can molecular and morphological markers tell us about plant hybridization? *Oxford Surv. Evol. Biol.* In press
91. Rieseberg LH, Zona S, Abernomb L, Martin TD. 1989. Hybridization in the island endemic, Catalina mahogany. *Conserv. Biol.* 3:52-8
92. Rogers CE, Thompson TE, Seiler GJ. 1982. *Sunflower Species of the United States*. Bismarck: Natl. Sunflower Assoc. 75 pp.
93. Sampson JF, Hopper SD, James SH. 1989. The mating system and population genetic structure in a bird-pollinated mallee, *Eucalyptus rhodantha*. *Heredity* 63:383-93
94. Schaal BA, Levin DA. 1977. The demographic genetics of *Liatris cylindracea*. *Am. Nat.* 110:191-206
95. Simberloff D. 1988. The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.* 19:473-511
96. Slatkin M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236:787-92
97. Slatkin M, Barton NH. 1989. A comparison of three indirect methods for estimating average levels of gene flow. *Evolution* 43:1349-68
98. Small E. 1984. Hybridization in the domesticated-weed-wild complex. In *Plant Biosystematics*, ed. WF Grant, pp. 195-210. Toronto: Academic Press. 674 pp.
99. Soltis PS, Soltis DS, Tucker TL, Lang FA. 1992. Allozyme variability is absent in the narrow endemic *Bensoniella*

- oregona* (Saxifragaceae). *Conserv. Biol.* 6:131–34
100. Soulé ME. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In *Conservation Biology: An Evolutionary-Ecological Perspective*, ed. ME Soulé, BA Wilcox, pp. 151–69. Sunderland, Mass: Sinauer. 345 pp.
101. Soulé ME, Kohm KA. 1989. *Research Priorities for Conservation Biology*. Covelo, Calif: Island. 97 pp.
102. Stace C. 1975. *Hybridization and The Flora of The British Isles*. London: Academic. 626 pp.
103. Stace C. 1991. *New Flora of The British Isles*. Cambridge: Cambridge Univ. Press. 1266 pp.
104. Svensson L. 1990. Distance-dependent regulation of stamen number in crosses of *Scleranthus annuus* (Caryophyllaceae) from a discontinuous population. *Am. J. Bot.* 77:889–96
105. Sytsma KJ, Schaal BA. 1985. Genetic variation, differentiation, and evolution in a species complex of tropical shrubs based on isozymic data. *Evolution* 39: 582–93
106. Templeton AR. 1986. Coadaptation and outbreeding depression. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. M. E. Soulé, pp. 105–16. Sunderland, Mass: Sinauer. 584 pp.
107. Templeton AR, Hemmer H, Mace G, Seal US, Shields WM, Woodruff DS. 1986. Local adaptation, coadaptation, and population boundaries. *Zoo Biol.* 5:115–25
108. Turner ME, Stephens JC, Anderson WW. 1982. Homozygosity and patch structure in plant populations as a result of nearest-neighbor pollination. *Proc. Natl. Acad. Sci. USA* 79: 203–07
109. van Treuren R, Bijlsma R, Ouborg NJ, van Delden W. 1993. The effects of population size and plant density on outcrossing rates in locally endangered *Salvia pratensis*. *Evolution* In press
110. van Treuren R, Bijlsma R, Ouborg NJ, van Delden W. The significance of genetic erosion in the process of extinction. IV. Inbreeding depression and heterosis effects due to selfing and outcrossing in *Scabiosa columbaria*. *Evolution*. In press
111. van Treuren R, Bijlsma R, van Delden W, Ouborg NJ. 1991. The significance of genetic erosion in the process of extinction. I. Genetic differentiation in *Salvia pratensis* and *Scabiosa columbaria* in relation to population size. *Heredity*. 66:181–89
112. Varvio S-L, Chakraborty R, Nei M. 1986. Genetic variation in subdivided populations and conservation genetics. *Heredity* 57:189–98
113. Vavrek MC, McGraw JB, Bennington CC. 1991. Ecological genetic variation in seed banks. III. Phenotypic and genetic differences between young and old seed populations of *Carex bigelowii*. *J. Ecol.* 79:645–62
114. Wagner DB, Allard RW. 1991. Pollen migration in predominantly self-fertilizing plants: barley. *J. Hered.* 82:302–04
115. Waller DM, O'Malley DM, Gawler SC. 1987. Genetic variation in the extreme endemic *Pedicularis furbishiae* (Scrophulariaceae). *Conserv. Biol.* 1: 335–40
116. Waser NM. 1993. Population structure, optimal outbreeding, and assortative mating in angiosperms. In *The Natural History of Inbreeding and Outbreeding, Theoretical and Empirical Perspectives*, ed. N. W. Thornhill, Chicago: Univ. Chicago Press. In press
117. Waser NM, Price MV. 1985. Reciprocal transplant experiments with *Delphinium nelsonii* (Ranunculaceae): evidence for local adaptation. *Am. J. Bot.* 72:1726–32
118. Waser NM, Price MV. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* 43:1097–109
119. Widen B, Andersson S. 1993. Quantitative genetics of life-history and morphology in a rare plant, *Senecio integrifolius*. *Heredity*. In press
120. Wright S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159



CONTENTS

CHAOS IN ECOLOGY: IS MOTHER NATURE A STRANGE ATTRACTOR?, <i>Alan Hastings, Carole L. Hom, Stephen Ellner, Peter Turchin, and H. Charles J. Godfray</i>	1
GENETICS AND EVOLUTION OF PHENOTYPIC PLASTICITY, <i>Samuel M. Scheiner</i>	35
PATTERNS OF SEED LONGEVITY AND GERMINATION IN THE TROPICAL RAINFOREST, <i>C. Vázquez-Yanes and A. Orozco-Segovia</i>	69
HYPOTHESES ON THE ORIGINS OF MARINE LARVAE, <i>Richard R. Strathmann</i>	89
THE EVOLUTION OF HOUSE MICE, <i>P. Boursot, J.-C. Auffray, J. Britton-Davidian, and Francois Bonhomme</i>	119
CONGRUENCE BETWEEN MOLECULAR AND MORPHOLOGICAL PHYLOGENIES, <i>Colin Patterson, David M. Williams, and Christopher J. Humphries</i>	153
SIBLING SPECIES IN THE SEA, <i>Nancy Knowlton</i>	189
POPULATION GENETIC CONSEQUENCES OF SMALL POPULATION SIZE: IMPLICATIONS FOR PLANT CONSERVATION, <i>Norman C. Ellstrand and Diane R. Elam</i>	217
AVIAN MOLECULAR SYSTEMATICS, 1970s TO 1990s, <i>Frederick H. Sheldon and Anthony H. Bledsoe</i>	243
HIGHER LEVEL SYSTEMATICS OF EUTHERIAN MAMMALS: AN ASSESSMENT OF MOLECULAR CHARACTERS AND PHYLOGENETIC HYPOTHESES, <i>Rodney L. Honeycutt and Ronald M. Adkins</i>	279
PHYLOGENETIC CONSTRAINT IN EVOLUTIONARY THEORY: HAS IT ANY EXPLANATORY POWER?, <i>Mary C. McKittrick</i>	307
REPRODUCTIVE TRAITS AND MALE FERTILITY IN PLANTS: EMPIRICAL APPROACHES, <i>Allison A. Snow and Paul O. Lewis</i>	331
THE PHENOLOGY OF TROPICAL FORESTS: ADAPTIVE SIGNIFICANCE AND CONSEQUENCES FOR PRIMARY CONSUMERS, <i>Carel P. van Schaik, John W. Terborgh, and S. Joseph Wright</i>	353

vi CONTENTS (*continued*)

DYNAMIC MODELS OF ENERGY ALLOCATION AND INVESTMENT, <i>Nicolas Perrin and Richard M. Sibly</i>	379
EVOLUTIONARY AND ECOLOGICAL ASPECTS OF PHOTOSYNTHETIC PATHWAY VARIATION, <i>James R. Ehleringer and Russell K. Monson</i>	411
THE EVOLUTION OF THE SELFING RATE IN FUNCTIONALLY HERMAPHRODITE PLANTS AND ANIMALS, <i>Philippe Jarne and Deborah Charlesworth</i>	441
TERTIARY MAMMAL EVOLUTION IN THE CONTEXT OF CHANGING CLIMATES, VEGETATION, AND TECTONIC EVENTS, <i>Christine M. Janis</i>	467
MINIATURIZATION OF BODY SIZE: ORGANISMAL CONSEQUENCES AND EVOLUTIONARY SIGNIFICANCE, <i>James Hanken and David B. Wake</i>	501
CYTONUCLEAR DISEQUILIBRIA IN HYBRID ZONES, <i>Jonathan Arnold</i>	521
PHYSICAL-BIOLOGICAL INTERACTIONS INFLUENCING MARINE PLANKTON PRODUCTION, <i>Kendra L. Daly and Walker O. Smith, Jr.</i>	555
HISTORICAL PERSPECTIVES IN ECOLOGY AND EVOLUTIONARY BIOLOGY: THE USE OF PHYLOGENETIC COMPARATIVE ANALYSES, <i>Donald B. Miles and Arthur E. Dunham</i>	587
INDEXES	
SUBJECT INDEX	620
CUMULATIVE INDEX OF CONTRIBUTING AUTHORS	641
CUMULATIVE INDEX OF CHAPTER TITLES	643