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September 10, 2010

DRECP Independent Science Advisors
1516 Ninth Street
Sacramento, CA 95814-5512

RE: Comments on the Independent Science Advisors Report Docket No. 09-RENEW EO-01.

Dear Science Advisors,

The Center for Biological Diversity greatly appreciates the indisputably science-based information but forth in the *Draft Recommendations of Independent Science Advisors for The California Desert Renewable Energy Conservation Plan (DRECP) - DRECP-1000-2010-008, August 2010*. We look forward to having those recommendations adopted by the DRECP as it moves forward in the process.

We have three additional suggestions for the science advisors to consider including in the final version of the *Recommendations* as follow:

1) Survey data from the current "fast-track" solar projects have documented potentially "new" species. These new species, while not officially described and therefore "recognized" by the scientific community, typically have very restricted ranges. Therefore, in the future and certainly within the lifetime of the plan, once recognized, they may represent an endemic, rare or otherwise "species of special concern". Recommendations describing mechanisms on how to treat these "newly discovered" species would be very useful and benefit protection of the planning area's biodiversity (a goal of the plan).

2) In the past, transplantation of rare plants has been tried as a mitigation strategy. Literature on the issue to date indicates significant failures (Fiedler 1991). Despite morphological successes (i.e. plants successfully transplanted and reproducing), Krauss et al. (2002) found that genetically, the transplantation effectively degraded the genetics of one rare plant species. Recommendations on transplantation of rare plants would be useful.

3) In the recent past, avoidance measures have been proposed to conserve rare plants in "halos" or Special-Status Plant Protection Areas – areas *within* a proposed project site where disturbance would be limited. However literature identifies fragmentation as a significant threat not only of the plant habitat itself (Honnay and Jacquemyn 2007, Matthies et al. 2004, Debinski and Holt 2000, Ellstrand and Elam 1993) but the pollinator habitat, which is crucial for many plants' reproduction (Kearns et al. 1998). Recommendations on how to effectively conserve rare plants in particular would also be useful.

Guidance on these important issues would be immensely helpful and we appreciate, in advance, the panels' expert opinion on them.

Sincerely,

Ileene Anderson
Biologist

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and a hardcopy will be sent to the address below:
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Dockets Office, MS-4
Docket No. 09-RENEW EO-01
1516 Ninth Street
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References included as attachments

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Review

A Survey and Overview of Habitat Fragmentation Experiments

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Abstract: *Habitat destruction and fragmentation are the root causes of many conservation problems. We conducted a literature survey and canvassed the ecological community to identify experimental studies of terrestrial habitat fragmentation and to determine whether consistent themes were emerging from these studies. Our survey revealed 20 fragmentation experiments worldwide. Most studies focused on effects of fragmentation on species richness or on the abundance(s) of particular species. Other important themes were the effect of fragmentation in interspecific interactions, the role of corridors and landscape connectivity in individual movements and species richness, and the influences of edge effects on ecosystem services. Our comparisons showed a remarkable lack of consistency in results across studies, especially with regard to species richness and abundance relative to fragment size. Experiments with arthropods showed the best fit with theoretical expectations of greater species richness on larger fragments. Highly mobile taxa such as birds and mammals, early-successional plant species, long-lived species, and generalist predators did not respond in the "expected" manner. Reasons for these discrepancies included edge effects, competitive release in the habitat fragments, and the spatial scale of the experiments. One of the more consistently supported hypotheses was that movement and species richness are positively affected by corridors and connectivity, respectively. Transient effects dominated many systems; for example, crowding of individuals on fragments commonly was observed after fragmentation, followed by a relaxation toward lower abundance in subsequent years. The three long-term studies (⩾14 years) revealed strong patterns that would have been missed in short-term investigations. Our results emphasize the wide range of species-specific responses to fragmentation, the need for elucidation of behavioral mechanisms affecting these responses, and the potential for changing responses to fragmentation over time.*

Sondeo y Revisión de Experimentos de Fragmentación de Hábitat

Resumen: *La destrucción y la fragmentación del hábitat son las causas fundamentales de muchos problemas de conservación. Realizamos un sondeo de la literatura y examinamos de cerca la comunidad ecológica para identificar estudios experimentales sobre la fragmentación de hábitats terrestres y para determinar si emergen temas homogéneos de estos estudios. Nuestro sondeo revela que existen 20 estudios experimentales de fragmentación en el ámbito mundial. La mayoría de los estudios enfocan en los efectos de la fragmentación sobre la riqueza de especies, o en la(s) abundancia(s) de ciertas especies en particular. Otros temas importantes fueron el efecto de la fragmentación sobre las interacciones interespecíficas, el papel de los corredores y la conectividad del paisaje en los movimientos individuales y la riqueza de especies y la influencia de los efectos de bordes sobre los servicios proporcionados por el ecosistema. Nuestras comparaciones muestran una carencia notable de homogeneidad en los resultados de los estudios, especialmente en lo referente a la riqueza y a la abundancia de especies, y su relación con el tamaño de los fragmentos. Experimentos con artrópodos demostraron que existía un mejor ajuste entre los valores teóricos esperados y los valores reales de aumentos en la riqueza de especies en fragmentos grandes. Los taxones altamente móviles (por ejemplo, aves y mamíferos), las especies de plantas en sucesión temprana, las especies de gran longevidad y los depredadores generalistas no respondieron de la manera "esperada". Entre las razones que explican estas diver-*

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gencias se incluyen los efectos de bordes, la liberación competitiva en los fragmentos de hábitat y la escala espacial del experimento. Una de las hipótesis más aceptadas establece que el movimiento y la riqueza de especies son afectadas positivamente por los corredores y la conectividad, respectivamente. Algunos efectos pasajeros dominaron muchos sistemas; por ejemplo, el hacinamiento de individuos en fragmentos se observó a menudo después de la fragmentación, seguido de un disminución de la abundancia en los años posteriores. Los tres estudios a largo plazo (=14 años) revelaron fuertes patrones que hubieran sido ignorados en investigaciones a corto plazo. Nuestros resultados señalan el amplio rango de respuestas especie-específicas, la necesidad de elucidar mecanismos de comportamiento que afectan las respuestas a la fragmentación y el potencial de respuestas cambiantes a la fragmentación a lo largo del tiempo.

Introduction

Given the importance of habitat fragmentation in conservation, it is not surprising that there exists a burgeoning literature based on observational studies of fragmented landscapes (e.g., Wilcove et al. 1986; Quinn & Harrison 1987; Gibbs & Faaborg 1990; Blake 1991; McCoy & Mushinsky 1994) and a substantial theoretical literature on the population and community effects of fragmentation (e.g., Fahrig & Paloheimo 1988; Doak et al. 1992; Nee & May 1992; Adler & Nuernberger 1994; Tilman et al. 1994; With & Crist 1995). In contrast, fewer researchers have deliberately created an experimentally fragmented landscape and then assessed the ecological consequences of the fragmentation (Margules 1996). It is easy to see why. Manipulation of entire landscapes tends to be large in scale, laborious, and costly. Yet the difficulty and expense of large-scale spatial experiments makes it particularly important that whatever data they generate be used to address general issues in ecology. In principle, fragmentation experiments could provide a rich testing ground for theories and methodologies dealing with spatiotemporal dynamics (Tilman & Kareiva 1997). Moreover, because of the logistical difficulty of such experiments, synthesis across studies may help provide guidelines and cautionary lessons for the design of future landscape experiments.

We present the results from a survey of studies conducted worldwide in experimentally fragmented habitats. By our definition, an experiment involves a deliberate manipulation of the landscape, usually with an eye toward assessing a particular hypothesis. In many descriptive fragmentation studies, researchers cannot control attributes such as patch size, degree of replication, site initiation, and position on the landscape because they are investigating the effects of landscape manipulation (e.g., clearcutting in logging or plowing in agriculture) conducted by others. Thus, we excluded such studies from our review. We concentrated on terrestrial systems because of the major differences in the dynamics of colonization between terrestrial and aquatic systems.

Methods

We conducted a literature survey of the major ecological journals (*American Naturalist, Biological Conservation, BioScience, Canadian Journal of Zoology, Conservation Biology, Ecography, Ecological Applications, Ecological Modeling, Ecological Monographs, Ecology, Evolutionary Ecology, Forest Science, Heredity, Journal of Animal Ecology, Journal of Biogeography, Journal of Mammalogy, Landscape Ecology, Nature, Oecologia, Oikos, Theoretical Population Biology,* and *Trends in Ecology and Evolution*) since 1984 using the keyword *fragmentation*. We also canvassed the ecological community using the Internet (CONSBIO listserver) and made informal contact with many colleagues. After compiling a list of candidate studies, we sent out a survey to the authors of the studies which asked questions about experimental design, focal organisms of study, hypotheses being tested, study length, and practical issues such as how the integrity of the experiment was maintained. We summarized the results in the form of a vote count tally of the number of times the hypothesis was supported. We believe that a more formal meta-analysis (e.g., Gurevitch & Hedges 1993) of these experiments is not yet warranted because of the relatively small number of studies and because of the heterogeneity among study designs, spatial and temporal scales, and methodological protocols.

Results

Replication and Temporal Span

Based on our criteria for fragmentation experiments, we identified 20 experimental studies; 6 were conducted in forests and 14 were conducted in grasslands or old fields. The experimental studies clustered into evaluations of five broad focal issues: species richness, the interplay of connectivity versus isolation, individual species behavior, demography, and genetics. They tested six major hypotheses: (1) species richness increases with area, (2) species abundance or density increases with area, (3) interspecific interactions are modified by fragmentation, (4) edge effects influence ecosystem services, (5) corridors enhance movement between fragments, and (6) connectivity between fragments increases species richness. For ease in following the discussion of the experiments included in our review (compiled in Table 1), we include within the text a number in brackets corresponding to the experiment number in Table 1.

The number of fragmentation experiments and the length of time for which they have been conducted have increased substantially in recent years (Table 1). A decade ago there were just 3 studies extant; at present 14 studies are ongoing. The geographic distribution of the 20 studies was primarily North America and Europe. The spatial scale (Fig. 1) ranged from grassland patches of <1 m^2 (Quinn & Robinson 1987 [2]) to Amazonian rainforest fragments of 1000 ha (Bierregaard et al. 1992 [1]). Replication (Fig. 1) varied from 1 to 160 per category of patch size. Patch sizes were chosen relative to the questions being addressed and the organism(s) of study. Generally, as the landscape scale increased, there were fewer replicates at larger fragment sizes. There was a threshold of decrease in degree of replication at roughly 0.2 ha; above this size, the number of replicates was usually <10. This weakens the statistical power of conclusions about the effects of large fragment size. The temporal spans for these studies ranged from 1 to 19 years, with a mean of just over 6 years (Table 1). Little experimental data exist on the long-term consequences of habitat fragmentation. Three experiments have been in progress for over a decade, and eight have been in progress for 5–10 years. The remaining projects were run for 3 years or less.

These experiments contain taxonomic and habitat biases. Only a few studies explicitly focused on plant population and community dynamics (Table 2). Among animals, there was a heavy emphasis on songbirds and small mammals. A number of studies focused closely on particular species, but few analyzed in detail the effects of fragmentation on pairwise or multispecies interactions (Kareiva 1987 [17] is a notable exception). Several of these projects examined responses across a variety of taxonomic groups simultaneously (Bierregaard et al. 1992 [1]; Margules 1992 [4]; Robinson et al. 1992 [3]; Baur & Erhardt 1995 [19]; D. Huggard, personal communication [6]). There also were habitat biases in that most studies were conducted in either forest, grassland, or old fields. This may reflect the economics and mechanics of creating and maintaining experimental patches, such as using mowing in old fields or grassland and relying upon forestry practices or clearcutting in forested biomes.

Predictions that Work

Numerous studies reported results that supported theoretical expectations; but many revealed effects contrary to initial theoretical expectations. Here we summarize results relative to the hypotheses tested (Table 2).

SPECIES RICHNESS

Following from the theory of island biogeography (MacArthur & Wilson 1967), species richness in habitat fragments is expected to be a function of island size and degree of isolation. Smaller, more isolated fragments are expected to retain fewer species than larger, less isolated habitat tracts (Diamond 1975; Wilson & Willis 1975; Terborg 1976). A major focus of these studies has been the relationship among habitat size, species richness, and individual species' abundances.

Initial theoretical expectations regarding increased species richness with increasing area were supported in only 6 out of 14 examples (not including 3 taxa that exhibited changing patterns over time). In cases in which the hypotheses were upheld, the effects were often striking. For example, even in a 100-ha tropical forest fragment, a beetle community was recognizably different in composition and lower in species richness than those on control sites in continuous forest (Laurance & Bierregaard 1996 [1]). Collinge (1995 [8]) found that insect species diversity was lowest in the smallest fragments and highest in the largest fragments. In a comparison of several types of fragmented landscapes, Collinge and Forman (1998 [8]) found that large-bodied, initially rare species were concentrated in the remaining larger core habitats, as opposed to areas where a central portion of habitat was removed. T. Crist (personal communication [11]) found a similar decrease in arthropod species richness with increasing fragmentation of an old field and determined that the pattern was driven primarily by the loss of rare species. In an old-field study [3] in Kansas, larger patches had higher species richness of butterflies, but small mammals and plants tended to show less consistent differences in species richness among patch sizes (Robinson et al. 1992; Holt et al. 1995*a*, 1995*b*). Baur and Erhardt (1995 [19]) found that, after 2 years, isolated grassland fragments were less frequently occupied by various gastropod species than were control patches, leading to lower species richness in the fragments. This set of studies provides a reasonable match with theoretical expectations.

Comparable to the effect of area on species richness, one might expect to observe area effects on genetic diversity within species; smaller fragments should have lower effective population sizes, higher rates of genetic drift, and fewer immigrants (Jaenike 1973). In the experimental studies in our survey, the effect of fragmentation on genetic variation was studied infrequently. Baur and Erhardt (1995 [19]), however, found reduced fecundity and genetic diversity among herbaceous plant species in isolated patches. Interactions between plants and pollinators also exhibited modifications, with potential

Table 1. A summary of fragmentation experiments with contact persons, references, biomes, dates of initiation and conclusion, patch sizes and replication, and other pertinent data.

Experiment no. and project name or biome	*Patch habitat*	*Matrix habitat*	*Institutional affiliation*	*Time span*	*Fragment sizes (replication)*	*Preexisting matrix*	*Community focus*	*Reference or contact*
1. Biological dynamics	tropical rainforest	clearcut	National Museum of History, Smithsonian Institution	1980–present (19 years)	1 ha (8), 10 ha (8),100 ha (5), 200 ha (1), 1000 ha (3)	yes	yes	Bierregaard et al. 1992; Bierregaard & Stouffer 1997
2. California grassland	California annual grassland	mowed grass	University of California, Davis	1983–1987 (4 years)	2 m^2 (32), 8 m^2 (8), 32 m^2 (2)	yes	yes	Quinn & Robinson 1987; Robinson et al. 1995
3. Kansas fragmentation study	Kansas old field	mowed grass	University of Kansas	1983–present (16 years)	50 × 100 m (6), 12 × 24 m (18), 4 × 8 m (82)	no	yes	Holt et al. 1995a, 1995b; Robinson et al. 1992
4. Wog Wog study	eucalypt forest	pine plantation	CSIRO Division of Wildife and Ecology	1985–present (14 years)	0.25 ha (6), 0.875 ha (6), 3.062 ha (6)	yes	yes	Margules 1992; Margules 1996
5. Groenvaly experiment	South African grassland	pine plantation	University of Pretoria, South Africa	1994–present (5 years)	0.25 ha (6), 0.875 ha (6), 3.062 ha (6)	yes	yes	Jaarsveld, personal communication
6. Kamloops project	Canadian subalpine forest	clearcut	British Columbia Ministry of Forests	1995–present (3 years)	0.1 ha (160), 1 ha (27), 10 ha (3)	yes	yes	Vyse 1997; Klenner & Huggard 1997
7. Missouri Ozark forest ecosystem project	Missouri Ozark hardwood forest	clearcut	Missouri Department of Conservation, University of Missouri	1990–present (9 years)	300 ha (2), 800 ha (1)	yes	yes	Kurzejaski et al. 1993
8. Colorado grassland	Colorado short grass prairie	mowed grass	University of Colorado	1992–1994 (2 years)	1 m^2 (18), 10 m^2 (18), 100 m^2 (18)	yes	yes	Collinge 1995
9. Boreal mixed-wood dynamics project	Canadian boreal mixed-woods	clearcut	University of British Columbia, University of Alberta, Edmonton	1993–present (6 years)	1, 10, 40, 100 ha (3 each)	yes	yes	Schmiegelow & Hannon 1993; Schmiegelow et al. 1997
10. Savannah River Site corridor project	clearcut	pine forest	University of Georgia, Iowa State University, U.S. Forest Service	1994–present (5 years)	128 × 128 m (27) with differing corridor lengths	yes	yes	Haddad 1997; Danielson and Hubbard (2000)
11. Miami University fragmentation project	Ohio old field	mowed grass	Miami University	1995–present (5 years)	2 × 2 m (36), 9 × 9 m (36), 13 × 13 m (36)	yes	yes	Crist & Golden, personal communication
12. German fragmentation study	Bavarian clover patches	crop fields and meadows	Gottingen University	1992–present (7) years	1.2 m^2 (18) with separation varying	yes	yes	Kruess & Tscharntke 1994
13. Blandy farm fragmentation study	Virginia old field	mowed grass	University of Virginia	1990–present (9 years)	1 ha (4), 0.25 ha (4), 0.63 ha (4)	no	no	Bowers & Dooley 1993
14. Vole behavior and fragmentation	alfalfa patches	mowed grass	Oregon State University	1994 (ongoing 4-month experiments)	25 × 25 m (4), 12.5 × 12.5 m (32), 5 × 5 m (100)	no	no	Wolff et al. 1997
15. Evensted research station	Norwegian meadows	mowed grass	University of Oslo, Norwegian Forest Research Institute, Agricultural University of Norway	1982–1989 (6 years)	15 × 20 m (4), 15 × 45 m (4), 0.5 ha (2)	no	no	Ims et al. 1993

continued

Table 1. (continued)

Experiment no. and project name or biome	*Patch habitat*	*Matrix habitat*	*Institutional affiliation*	*Time span*	*Fragment sizes (replication)*	*Preexisting matrix*	*Community focus*	*Reference or contact*
16. Long Ashton	British croplands	mowed grass	Institute of Arable Crops Research	1995–present (4 years)	9 × 9 m (36), 27 × 27 m (5)	no	yes	Powell
17. Predator-prey interactions and fragmentation	New York goldenrod monoculture	mowed grass	Cornell University	1982–1985 (3 years)	20 m^2 (3), 6 m^2 (30)	no	no	Kareiva 1987
18. Ohio old-field project	Ohio old field	mowed grass	Miami University	annual	160 m^2 (4), 40 m^2 (16)	no	no	Barrett et al. 1995
19. Swiss Jura mountains	European calcareous grassland	mowed grass	University of Basel, Switzerland	1993–present (6 years)	4.5 × 4.5 m (24), 1.5 × 1.5 m (24), 0.5 × 0.5 m (48)	yes	yes	Baur & Erhardt 1995
20. Root vole sex ratio	Norwegian grassland	mowed grass	University of Oslo	1990–1995 (5 years)	0.0225 ha (12), 0.675 ha (4)	yes	no	Aars et al. 1995

ramifications for genetic diversity. For example, butterflies visited flowers less frequently in isolated patches, thus leading to reduced fecundity and possibly lower plant genetic diversity.

DENSITY AND ABUNDANCE OF SPECIES

The negative effects of fragmentation on species richness arise in part because of lower-level effects on population abundance and so should be evident even in those species that do not become extinct. The simplest a priori expectation is that, for habitat specialists restricted to the fragments and unable to use the matrix habitat, fragmentation reduces density. The mechanism for this reduced density could be increased demographic stochasticity or the disruption of metapopulation dynamics. The alternative hypothesis, however, is that species move from the matrix habitat to the remaining habitat patches after a disturbance, such that "crowding" ensues in the patches (Whitcomb et al. 1981; Fahrig & Paloheimo 1988; Fahrig 1991). Our summary refers to density and abundance because some authors presented their results as density, whereas others presented results as abundance or trapping success per unit time.

Species abundance decreased with fragmentation in 6 out of 13 examples. For instance, Margules and Milkovits (1994 [4]) found that the abundance of amphipods (family Talltridae) decreased markedly in remnant forest patches relative to controls and that this effect was more dramatic on smaller remnants than on larger ones. In the Kansas project [3], the cotton rat (*Sigmodon hispidus*) and the white-footed mouse (*Peromyscus leucopus*) were differentially more abundant in larger patches (Foster & Gaines 1991; Robinson et al. 1992; Schweiger et al. 1999). H. Norowi (personal communication [16]) similarly found that weevil and parasitoid densities were consistently greater in contiguous habitat patches than in fragmented patches of equivalent area.

The density of tree seedlings declined significantly from continuous forest to forest fragments in the Amazonian Biological Dynamics Project [1] (Benitez-Malvido 1998). These results demonstrate the effect of fragmentation on key life-history stages in trees. In the Kansas study [3], which involves old-field succession, colonization by woody plant species is proceeding more rapidly in larger patches (Holt et al. 1995*b*; Yao et al. 1999). Thus, changes at the level of individual species can often be discerned, even when coarser, whole-community effects of fragmentation are not apparent (Robinson et al. 1992).

INTERSPECIFIC INTERACTIONS AND ECOLOGICAL PROCESSES

Spatial dynamics can have profound effects on individual behavior (e.g., Hanski et al. 1995; Redpath 1995) and interspecific interactions such as predation (Aizen & Feinsinger 1994; Tilman & Kareiva 1997), so it is sensi-

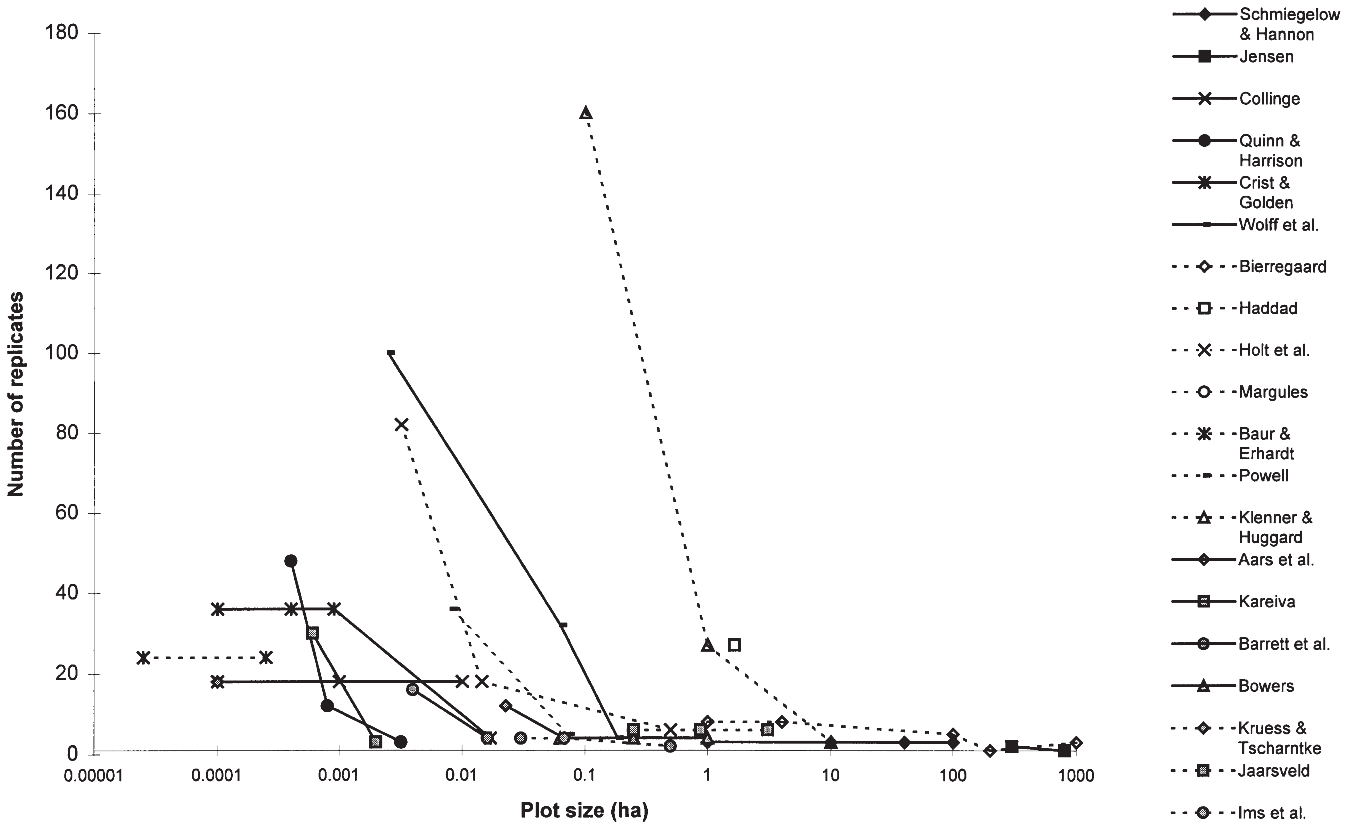

Figure 1. Frequency distribution of fragmentation studies relative to plot size.

ble to expect that the effects of habitat fragmentation may be mediated or exacerbated through shifts in such interactions. Kareiva (1987 [17]) demonstrated this effect by performing experiments on a predator-prey interaction between an aphid and a coccinellid predator in monocultures of *Solidago*. The fragmented treatment had more frequent aphid outbreaks, apparently because fragmentation disrupted the ability of the predator to aggregate rapidly at localized clusters of the aphid in early phases of an outbreak. H. Norowi (personal communication [16]) found that the rate of weevil parasitism varied with parasitoid species and the spatial scale of analysis. W. Powell (personal communication [16]) similarly found that carabid beetle assemblages in experimentally fragmented agroecosystems revealed significant spatial and temporal effects arising from altered predator-prey interactions within grassland patches.

EDGE EFFECTS

Another rule derived from the theory of island biogeography is that reserves should minimize the edge-to-area ratio to maximize the effective core area of the reserve. Increasing the amount of edge can make a reserve more vulnerable to invasion by exotic species and subject it to more extreme abiotic influences such as wind and temperature (Saunders et al. 1991). Physical changes associated with creating an edge can have profound effects on ecological processes. For instance, R. Bierregaard (personal communication [1]) documented that edge effects penetrate 300 m or more into a tropical forest remnant, and Didham (1997 [1]) showed that isolated patches have leaf-litter insect fauna substantially different than that of continuous forest.

In principle, the altered abiotic conditions associated with fragmentation can also influence ecosystem services such as nutrient cycling (Saunders et al. 1991). Three projects have addressed ecosystem consequences of fragmentation with varying results. Two forest projects found effects on nutrient cycling (Bierregaard et al. 1992 [1]; Klenner & Huggard 1997 [6]), whereas the Kansas old-field study [3] did not (Robinson et al. 1992). In the Biological Dynamics Project [1] and other forest studies, the contrast in abiotic conditions between fragments (e.g., tall forest) and the surrounding matrix (e.g., pasture) is dramatic. In other systems, there are less dramatic differences between the matrix and fragments, so one might expect ecosystem effects to be less noticeable.

Because fragmentation inevitably leads to the juxtaposition of qualitatively different habitats, flows of materials and individuals between them can indirectly exert profound influences on within-fragment communities

(Polis et al. 1997). In the Kansas study [3], for instance, generalist arthropod predators such as web-building spiders are more abundant in the fragments, particularly along edges, where they can profit from the aerial "drift" of insects from the surrounding productive, mown interstitial turf (T. Jackson et al., unpublished data). Smaller forest fragments similarly had greater community invasibility for successional tree species in the Biological Dynamics Project [1] (Benitez-Malvido 1998). Laurence et al. (1998) found that recruitment rates were markedly higher near forest edges and highest within 100 m of forest edges.

CORRIDORS AND MOVEMENT/CONNECTIVITY

Fragmentation creates barriers to dispersal (e.g., Mader 1984), and behavioral responses to fragmentation may underlie many observed effects at higher organizational levels such as populations and communities. Even narrow breaks (50–100 m) in continuous forest habitat produce substantial barriers to the movement of many species of birds and some insects. Of the five fragmentation experiments that directly tested the effects of corridors, all but one found that corridors enhanced movement for some of the species examined (Collinge 1995 [8]; Haddad 1997 [10]; Schmiegelow et al. 1997 [9]; Wolff et al. 1997 [14]). Collinge (1995 [8]) found that corridors slightly decreased the rate of species loss and that this effect was greatest in medium-sized fragments. In another experiment (Haddad 1999; Haddad & Baum 1999 [10]), three open-habitat butterfly species (*Juononia coenia, Phoebis sennae*, and *Euptoieta claudia*) reached higher densities in patches connected by corridors than in isolated patches. But the abundance of a fourth, generalist species, *Papilio troilus*, was insensitive to forest corridors.

Related to corridors is the effect of landscape pattern on movement, as expressed for instance in rates of colonization and dispersal. H. Norowi (personal communication [16]) found that the presence of a hedgerow on one side of an experimental patch affected the pattern of colonization of newly created habitat patches by one species of weevil (*Gymnetron pascuorum*). Kruess and Tscharntke (1994 [12]) found substantial distance effects on colonization by parasitoids in a clover field but only minor effects on colonization by herbivores. This led to release from parasitism on the isolated patches, analogous to the effects of fragmentation in the predator-prey interaction studied by Kareiva (1987 [17]). Parasitoid species that failed to establish tended to be those with low and variable populations. These patterns have persisted over several years (T. Tscharntke, personal communication).

There is a growing literature on small mammals focusing on the effects of experimental fragmentation on dispersal and home-range size. Diffendorfer et al. (1995*a,b* [3]) showed that fragmentation reduced the movement rates and altered spatial patterning of distances moved in several small-mammal species. Wolff et al. (1997 [14]) found that fragmentation reduced vole (*Microtus canicaudus*) movements considerably. Ims et al. (1993 [15]) found decreased home-range size and more home range overlap in small mammals on smaller patches. Harper et al. (1993 [18]) found that the shape of habitat patches affected the number of voles that dispersed when population densities were low but not when densities were high. Furthermore, the shape of the habitat patches affected the space-use behavior of resident voles. Bowers et al. (1995 [13]) examined the space-use behavior of voles (*Microtus pennsylvanicus*) and found that adult females at edges tended to have larger home ranges, body sizes, residence times, and reproductive rates than individuals in the interior of a patch. Bowers et al. (1995 [13]) suggest that this edge effect could account for the inverse patch-size effects on abundance for small mammals noted in several studies (e.g., Foster & Gaines 1991 [3]). Finally, Ims et al. (1993 [15]) studied the effects of fragmentation on aggressive and docile strains of voles (*Microtus oeconomus*) and found that different sex and age groups are likely to exhibit different spatial responses to fragmentation.

Predictions that Do Not Work

SPECIES RICHNESS

In a number of experiments, species richness either increased with or was unaffected by fragmentation. In most cases, these effects could be attributed to an increase in early-successional species, transient species, or edge effects (community "spillover" from surrounding habitats; Holt 1997). For instance, Schmiegelow et al. (1997 [9]) examined passerine data gathered before fragmentation and during the 2 years thereafter. Despite effects on turnover rates, they found no significant change in species richness as a result of harvesting, except in the 1-ha connected fragment treatment, where the number of species actually increased 2 years after isolation. This increase reflected transient species rather than species breeding in the patches, suggesting that buffer strips were being used as corridors.

In the Biological Dynamics Project [1], frog diversity increased after fragmentation because of unpredicted immigration by generalist species that flourished in the matrix of pasture surrounding the forest fragments (Laurance & Bierregaard 1996). The Wog Wog Study [4] in southeast Australia (Margules 1996; Davies & Margules 1998; Margules et al. 1998) revealed that different taxa had highly disparate responses to fragmentation, including a lack of response. Plant communities in several experiments have exhibited species-richness patterns contrary to the expectations of island biogeography models. Quinn and Robinson (1987 [2]) found increased flowering-plant and insect species richness with increasing habitat subdivision. They hypothesized that these patterns might reflect the effect of fragmentation on competition

Table 2. A vote-count summary of fragmentation-experiment results, separated by hypothesis tested.*

Project name	*Taxonomic group*	*Hypothesis supported*	*Reference or contact*
Species richness increases with area			
1. Biological dynamics	birds	yes	Bierregaard et al. 1992; Stouffer & Bierregaard 1995
	beetles	no	Laurance & Bierregaard 1996
	frogs	no	Laurance & Bierregaard 1996
	primates	yes	Bierregaard et al. 1992
2. California grassland	plants	no	Quinn & Robinson 1987; Robinson et al. 1995
	insects	no	Quinn & Robinson 1987; Robinson et al. 1995
3. Kansas fragmentation study	small mammals	no	Holt et al. 1995*a*, 1995*b*; Robinson et al. 1992
	plants	no	Robinson et al. 1992; Holt et al. 1995*a*, 1995*b*
	butterflies	yes	Holt et al. 1995*a*
4. Wog Wog study	millipedes	no, years 1–7; yes, years 7–present	Margules 1992
	frogs	yes, years 0–5; no, years 5–present	Margules 1996
	beetles	no	Davies & Margules 1998
8. Colorado grassland	insects	yes	Collinge 1995; Collinge & Forman 1998
9. Boreal mixed-wood dynamics project	birds	no, treatments and controls yes, isolated fragments	Schmiegelow et al. 1997
11. Miami University fragmentation project	insects	yes	Crist & Golden, personal communication
19. Swiss Jura mountains	gastropods	yes	Baur & Erhardt 1995
Species abundance or density increases with area			
1. Biological dynamics	trees (woody)	yes	Benitez-Malvido 1998
	trees (seedling recruitment)	no	Benitez-Malvido 1998
	beetles	yes	Bierregaard et al. 1992
	birds	no (short term); yes later	Bierregaard & Lovejoy 1989
3. Kansas fragmentation study	trees	yes	Holt et al. 1995*b*; Yao et al. 1999
	small mammals	mixed	Foster & Gaines 1991; Schweiger et al. 1999
4. Wog Wog study	amphipod density	yes	Margules & Milkovits 1994
	scorpions	no	Margules & Milkovits 1994
8. Colorado grassland	insects	no	Collinge & Forman 1998
9. Boreal mixed-wood dynamics project	birds	no, treatments and controls	Schmiegelow et al. 1997
		yes, isolated fragments	Schmiegelow et al. 1997
13. Blandy farm fragmentation study	small mammals	no	Bowers & Matter 1997; Dooley & Bowers 1998
14. Vole behavior and fragmentation	small mammals	no	Wolff et al. 1997
15. Evensted research station	small mammals	no	Ims et al. 1993
16. Long Ashton	weevils and parasitoids	yes	W. Powell, personal communication
17. Predator-prey interactions and fragmentation	insects	yes	Kareiva 1987
18. Ohio old-field project	small mammals	no	Barrett et al. 1995; Collins & Barrett 1997
Interspecific interactions are modified by fragmentation			
12. German fragmentation study	parasitoids	yes (less parasitism on far patches)	Kruess & Tscharntke 1994

continued

Table 2. (continued)

Project name	*Taxonomic group*	*Hypothesis supported*	*Reference or contact*
16. Long Ashton	beetles	yes	W. Powell, personal communication
17. Predator-prey interactions and fragmentation	insects	yes	Kareiva 1987
Edge effects influence ecosystem services			
1. Biological dynamics	nutrient cycling	yes	Bierregaard et al. 1992
6. Kamloops project	nutrient cycling	yes	Klenner & Huggard 1997
3. Kansas fragmentation study	nutrient pools	no	Robinson et al. 1992
Corridors enhance movement between fragments			
8. Colorado grassland	insects	yes	Collinge 1995
9. Boreal mixed-wood dynamics project	birds	no for Neotropical migrants yes for transient species	Schmiegelow et al. 1997
10. Savannah river site corridor project	butterflies	yes for some; no for others	Haddad 1997
	small mammals	no	Danielson & Hubbard 2000
14. Vole behavior and fragmentation	small mammals	yes	Wolff et al. 1997
Connectivity between fragments increases species richness			
8. Colorado grassland	insects	yes	Collinge 1995
9. Boreal mixed-wood dynamics project	birds	no for Neotropical migrants	Schmiegelow et al. 1997
		yes for transient species	Schmiegelow et al. 1997

* *Where multiple taxa were examined in a single study, there are multiple entries for the same experimental site.*

among plants. In small patches, for instance, short-statured plant species could persist in edges and priority effects could permit local dominance not possible in a single large patch. Robinson et al. (1995 [2]) also examined invasibility by a native California poppy (*Eschscholzia californica*) in these same plots and found the species-rich plots more invasible. Contributing factors included a positive effect of small-mammal disturbance and a negative effect of *Bromus diadrus* coverage.

Invasion by species from the surrounding matrix could lead to a temporary increase in species richness within patches, at least if extinction rates are slow. If smaller fragments experience higher disturbance rates, this could shift competitive regimes such that in some situations species richness is enhanced. During the first 8 years of the Kansas [3] old-field experiment, patch size had little effect on successional replacement of major plant functional groups. Rather, the main influence of patch size was on the spatial autocorrelation of herbaceous community structure and on local persistence of some rare or clonal plant species (Robinson et al. 1992; Holt et al. 1995*a*, 1995*b*; Heisler 1998). In contrast, patch size had substantial effects on the colonization and growth rate of woody species (Yao et al. 1999).

DENSITY AND ABUNDANCE OF SPECIES

In several fragmentation experiments, population densities increased on the smaller fragments, perhaps because of the crowding effects of fragmentation. This was especially prevalent in small-mammal studies but was also observed in birds and insects. Barrett et al. (1995 [18]) found vole densities to be greater in a more fragmented landscape. In a review of patch-size effects on small-mammal communities, Bowers and Matter (1997 [13]) noted that inverse relations between density and patch size are frequently observed, particularly at the smaller patch sizes used in experimental landscape studies.

In some cases, the unexpected effect of fragmentation on density seems to reflect the ability of a focal species to utilize both the matrix habitat and the fragment. For instance, Foster and Gaines (1991 [3]) observed a high density of deer mice on small fragments and substantial numbers in the intervening matrix. They interpreted this pattern as simply a reflection of habitat generalization, but more recent work (Schweiger et al. 1999) suggests that a combination of habitat generalization and competitive release on small patches may explain this density relationship.

There appears to be a complex relationship between patch fragmentation and social structure that may underlie some of the inverse-density relationships. For instance, Collins and Barrett (1997 [18]) found that fragmented patches of grassland support greater densities of female voles than unfragmented sites. Aars et al. (1995 [20]) found differences in sex ratios among some litters of root voles and speculated that resource conditions (as affected by fragmentation) could lead to such biases.

Dooley and Bowers (1998 [13]) found weak fragment-size effects on the density and recruitment of *Microtus pennsylvanicus* in a grassland fragmentation experiment. They postulate that higher recruitment rates on fragmented patches result from diminished social costs and enhanced food resources on fragments. Andreassen et al. (1998 [15]) also found complex behavioral responses of voles to habitat fragmentation. Wolff et al. (1997 [14]) found that habitat loss did not decrease adult survival, reproductive rate, juvenile recruitment, or population size in the gray-tailed vole (*Microtus canicaudus*); surviving voles simply moved into remaining fragments. An influx of unrelated females into habitat fragments, however, resulted in decreased juvenile recruitment in those fragments.

Crowding effects have also been observed after fragmentation in bird and insect communities. Schmiegelow et al. (1997 [9]) noted that this crowding effect disappeared for birds after the second year of their study. Margules and Milkovits (1994 [4]) found that two millipede species experienced population explosions after treatment in both the remnants and the intervening cleared area, but they returned to pretreatment levels after 7 years. Collinge and Forman (1998 [8]) found crowding effects on fragments in an insect community but did not collect data long enough to test for a temporal effect.

CORRIDORS AND MOVEMENT/CONNECTIVITY

A few studies showed movement patterns contrary to what are generally expected to be the effects of habitat fragmentation, patch shape, and corridors. Barrett et al. (1995 [18]) showed that patch shape does not markedly affect dispersal or demographic variables of the meadow vole (*Microtus pennsylvanicus*). Andreassen et al. (1998 [15]) found that the rate of interfragment movements of small mammals actually increases with habitat fragmentation. Even more surprisingly, Danielson and Hubbard (2000 [10]) found that the presence of corridors reduces the probability that old-field mice (*Peromyscus polionotus*) will leave a patch in a forest fragment. In this same landscape Haddad (1997 [10]) found one butterfly species that does not respond to corridors. Schmiegelow et al. (1997 [9]) showed that Neotropical migrants declined in all fragmented areas, regardless of connectivity. As one might imagine, the use of corridors and the effect of fragmentation on movement patterns seems to be highly species-specific. These results suggest a need for further study of the potentially complex interactions between fragmentation and individual behavior.

Logistical Problems and Considerations

We concentrated on the fruits of experimentation in the study of habitat fragmentation. But our survey did reveal recurrent problems with such experiments, which future workers attempting to conduct fragmentation experiments need to be aware of and consider in designing their experiments. These considerations are important in that they define the likely scope of the applicability of results from fragmentation experiments.

Common problems in orchestrating fragmentation experiments mentioned to us by a number of investigators in our survey included the costs and difficulty of adequate replication of large patches, the struggle to maintain patches, and the problems of identification of specimens in many species-rich taxa. Patches carved out of preexisting vegetation are likely to be heterogeneous in many respects; careful thought must be given to overlaying fragmentation treatments on preexisting heterogenous landscapes, especially with a low degree of replication. In cases in which patch sizes are large, costs and other problems with establishing the largest patches often result in low replication. In any system operating within a fixed area, there is a necessary trade-off among interpatch distance, patch size, and replication. Because of such constraints, out of the full domain of potential landscape configurations, experiments are likely to focus on only a modest swath of parameter space (Holt & Bowers 1999).

Maintenance of the experimental area also can be expensive, time-consuming, and uncertain. Collaboration between government agencies and/or private landowners and researchers is often key to establishing and maintaining a landscape for experimental purposes. In highly productive habitat such as tropical rainforest, the rate of secondary succession can be so high that it is difficult to keep patches "isolated" (e.g., Bierregaard et al. 1992). If the surrounding sea of vegetation is not completely inhospitable, this could skew results in experiments testing for the effects of isolation.

In small experimental fragments, the effects of sampling can be problematic, especially if multiple investigators are collecting data on several taxonomic groups. For example, to sample small patches without trampling the vegetation, G. Robinson (personal communication [2]) had to build portable scaffolds over the patches. Finally, taxonomic problems were noted by many investigators working on plants and insects (Holt et al. 1995*a* [3]; S. Collinge, personal communication [8]; C. Margules, personal communication [4]). This mundane problem is important if species-rich groups tend to have stronger responses to fragmentation.

Discussion

There was a considerable lack of consistency in results across taxa and across experiments. The two most frequently tested hypotheses, that species richness increases with fragment area and that species abundance or density increase with fragment area, showed entirely mixed results. Some of these discrepancies may be explained by differential relaxation times (Brown 1971) and rates of responses to fragmentation by different taxa. Most of the studies that fit initial theoretical expectations about the effects of fragmentation upon species richness involved arthropod assemblages. The species in these assemblages were typically small in body size (relative to the fragment sizes) and short in generation length (relative to the length of the fragmentation experiments). These assemblages might be expected to show responses over time scales commensurate with the time frame of typical field experiments. One of the more consistently supported hypotheses was that corridors supported connectivity between fragments. In four out of five cases, the presence of corridors enhanced movement for at least some of the species examined, and in two out of two examples the presence of corridors increased species richness in fragments.

Taxonomic groups that did not respond in the expected manner displayed a range of responses to fragmentation. Some examples include highly mobile taxa whose population-level responses may integrate over spatial domains much larger than that of a single fragment. At short time scales, behavioral responses by mobile organisms can generate idiosyncratic patterns. Crowding of individuals was commonly observed after fragmentation, followed by a relaxation in subsequent years. Other groups that responded differently than expected include long-lived species unlikely to show dramatic population responses in short-term experiments and taxa with generalized habitat requirements. Predicting fragmentation effects depends on a basic knowledge of the range of habitats that different taxa can utilize and on the factors limiting and regulating population abundance in unfragmented landscapes. The plethora of contradictory results for small mammals in fragmentation experiments seems to be caused by several factors, including habitat generalization, disparate responses among species to edges and corridors, and social interactions that may be modified by landscape changes.

Many of the "contrary" results we report may reflect the relatively short time span of the experiments. A number of studies used patches that lasted only one season or an annual cycle to examine changes in the behavior or demography of particular species. The advantage of this approach is that it permits a clearer evaluation of potential mechanisms underlying landscape effects. A disadvantage is that such experiments cannot evaluate the multiplicity of indirect feedbacks that occur in anthropogenically disturbed landscapes. Long-term experiments are vital because they reveal processes that are obscured at shorter time scales. The three long-term studies [1, 3, 4] each revealed strong phenomena that would have been missed in short-term investigations.

Some key findings of experimental habitat fragmentation studies might be difficult to achieve in purely observational studies, reflecting in part the value of good experimental controls and properly randomized designs. We do not imply that experimental fragmentation projects are more rigorous than observational studies. Experimental fragmentation studies often suffer from the intellectual costs of focusing on small spatial and temporal scales and the use of species that may not serve as good models for the effects of fragmentation on species of conservation concern. Although observational studies pay a price by lacking "controls," they nonetheless provide more realism with respect to landscape scale and species of concern. The value of having real controls, however, should not be underestimated; controls proved vital in interpreting results in many of these experiments (e.g., Robinson et al. 1995 [2]; Collins & Barrett 1997 [18]; Davies & Margules 1998 [4]; Laurance et al. 1998 [1]; Danielson & Hubbard 2000 [10]).

Future fragmentation studies should focus on understanding the mechanisms behind observed community- and population-level patterns. For example, a critical issue is how fragmentation affects dispersal and movement. Similarly, a better understanding of species interactions, such as plant-pollinator interactions or competition in fragmented landscapes, is essential. Analysis of the matrix habitat may be crucial for understanding the dynamics of remnant fragments. The most important determinant of which species are retained in isolated patches appears to be the interaction of patches with the surrounding habitat matrix (Bierregaard & Stouffer 1997 [1]; Tocher et al. 1997 [1]). There is a growing recognition that connection among habitats that differ in productivity and structure is often a crucial determinant of community dynamics (Holt 1996; Polis et al. 1997), and fragmentation experiments provide a natural forum for analyzing such dynamics. Finally, more analysis of how fragmentation influences genetic variation for both neutral alleles and traits related to fitness would be particularly valuable.

Choosing an appropriate landscape scale for the taxonomic group(s) of interest can have major implications for the findings of fragmentation studies. Communities are composed of species that experience the world on a vast range of spatial scales (Kareiva 1990; Holt 1993). In all the studies we reviewed, there were some mobile and/or large-bodied organisms for which the patches were small pieces of a fine-grained environment much smaller than a home range. Usually, however, some species will be present that experience the patches in a coarse-grained manner. An important challenge is to map out an intellectual protocol for applying these fine-scale experimental studies to scales that are more directly pertinent to conservation problems.

The studies described in our review provide a first step in understanding the effects of fragmentation. Our results, however, emphasize the wide range of species-specific responses and the potential for changing results over time. Fragmentation effects cascade through the community, modifying interspecific interactions, providing predator or competitive release, altering social relationships and movements of individuals, exacerbating edge effects, modifying nutrient flows, and potentially even affecting the genetic composition of local populations. Perhaps it is not surprising then that fragmentation shows inconsistent effects across the experimental studies of fragmentation to date.

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Note added in proof: Since this paper was written, we have become aware of an additional experimental study of fragmentation involving microinvertebrate species assemblages on moss patches on boulders. Gonzalez et al. showed strong effects of fragmentation on species diversity and population size (A. Gonzalez, J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047.).

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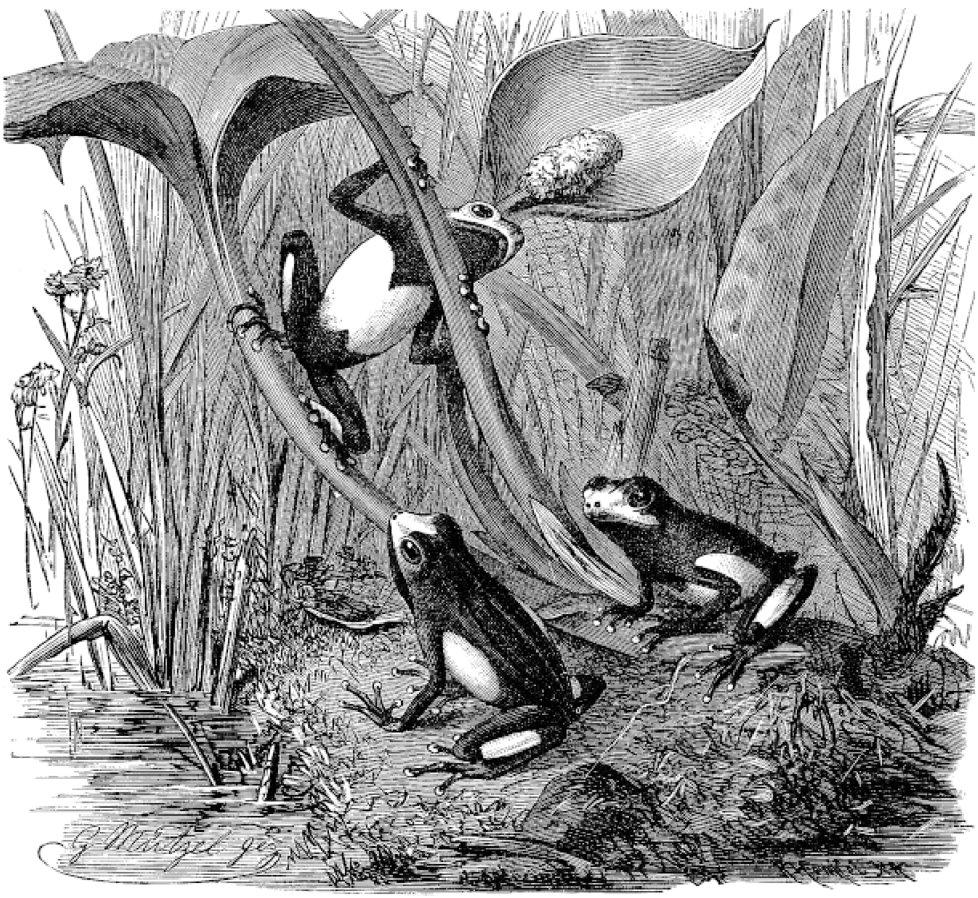

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POPULATION GENETIC CONSEQUENCES OF SMALL POPULATION SIZE: Implications for Plant Conservation

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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

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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 *Lisianthius 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 (*He*) 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
Acacia anomala (Chittering populations)	3–50	No	0.06	19
Eucalyptus caesia	7–580	Yes (P)	0.61	78
Eucalyptus crucis	4–300	Yes (P, A, H_e)	0.24	93
Eucalyptus parvifolia	20–1350	No	0.07	84
Eucalyptus pendens	27–3000	No	0.08	79
Eucalyptus pulverulenta	30–3000	Yes (P, A, H_e)	0.30	83
Halocarpus bidwillii	20–400,000	Yes (P, A, H_e)	0.04	13
Salvia pratensis	5–1500	Yes (P, A)	0.16	111
Scabiosa columbaria	14–100,000	Yes (P, A)	0.18	111
Washingtonia filifera	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 dudleyena*. 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

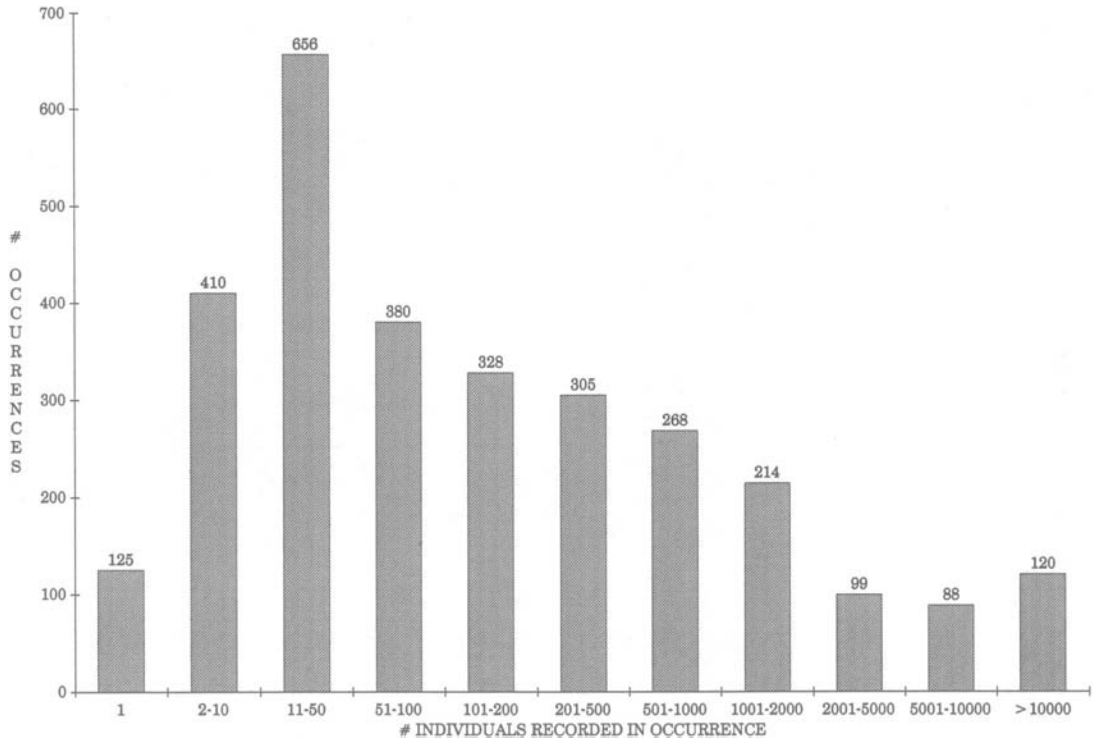

Figure 1 Number of individuals in occurrences of sensitive flora of California. (Each occurrence was assumed to constitute a single population. See text for more information.)

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 considerable 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 = 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 involved 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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FINAL REPORT

MITIGATION-RELATED TRANSPLANTATION, RELOCATION AND REINTRODUCTION PROJECTS INVOLVING ENDANGERED AND THREATENED, AND RARE PLANT SPECIES IN CALIFORNIA

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I. EXECUTIVE SUMMARY

To investigate the efficacy and overall success of transplantation, relocation, and reintroduction of California State-listed endangered, threatened, and rare species, a questionnaire was mailed to 377 individuals, state and federal agencies, and public and private institutions that potentially have been involved in transplantation, relocation, and reintroduction projects. One hundred sixty-eight questionnaires (168) were returned. Of these, twenty-four (24) individuals and/or agencies indicate that they have been directly involved in mitigation-related projects for California plants; one hundred fourteen (114) individuals and/or agencies have not. At minimum, this represents a 45% return rate for the questionnaire.

Files of California Department of Fish and Game's Endangered Plant Program were also reviewed to complete the survey. An additional 13 projects involving eight (8) State-listed species were identified as of these types. Information obtained from the Endangered Plant Program files supplemented 13 responses to the questionnaire.

This report summarizes the results of the questionnaire for each species identified by the respondents and information obtained from the Endangered Plant Program's files. A total of forty-six (46) projects were reviewed, involving fifty-three (53) transplantation, relocation and reintroduction attempts with forty (40) special status species. Of the plant species examined in this review, 25 (63%) are listed by the State as endangered, 3 (8%) are listed as threatened, 6 (15%) are listed as rare, and 6 (15%) are not listed by the State, but have some other form of protection or special status.

In addition, the 40 plant species reviewed belong to 21 plant families. Asteraceae represented the highest number of species involved (9; 23%), followed by the Brassicaceae (4; 10%). Eight (8) additional plant families were represented by two taxa, while ten (10) families were represented in this study by one taxon. The genus *Erysimum* had the greatest number of taxa (3) involved, followed by the genera *Brodiaea, Hemizonia, Lupinus*, and *Oenothera* (2 each).

Results of the survey indicate that of the 46 projects reviewed, 38 (83%) are mitigation-related, while eight (8) projects (17%) are research-related. Of the 53 manipulation attempts, forty-one (41; 77%) involved translocation (including relocation) of species of concern, nine (9) projects (17%) involved reintroduction, and 2 projects (4%) involved restoration of a population of a State-listed species. One additional project reviewed is a research-related project that has yet to include a transplantation, relocation or restoration component.

Thirty-six (36) projects have been implemented, while ten (10) projects are still in the planning stages. Seventeen projects (27%) are developments for housing, business parks, or recreational facilities initiated by private companies and corporations. Eleven projects (24%) are the result of state service operations, such as those by the California Department of Transportation and Department of Water Resources. The remaining projects are either initiated by county services (9%), private and public energy utilities (11%), or are research related. Of the total 46 projects, only 15 projects (33%) had explicitly defined criteria for success of the mitigation project, while the remaining 31 (67%) either had no criteria for success or the criteria were only vaguely defined.

Only 15% (8) of the 53 transplantation, relocation, or reintroduction attempts reviewed should be considered fully successful (13% of the 46 projects). Plant species for which the project was successful included *Amsinckia grandiflora, Dudleya cymosa* ssp. *marcescens, Holocarpha macradenia, Lasthenia burkei, Opuntia basilaris* var. *treleasei*, and *Sidalcea pedata*. However, of these eight (8) projects, only four (4) are mitigation-related. Therefore, the success rate of the mitigation-related transplantation, relocation, and reintroduction attempts is 8% (9% of the projects). An additional seven (7) transplantation projects (13%) (9 attempts [17%]) are considered partially successful, or of limited success. Twelve (12) projects (26%) are considered here to be unsuccessful, no information was found in the review of files for four (4) projects (9%), and the success of an additional sixteen (16) projects (35%) could not be evaluated because they are on-going or in the planning stages.

In a summary review of the successes and failures of transplantation, relocation and reintroduction of sensitive plant species in California, three broad recommendations can be made that are based on crucial aspects of the biology of imperiled plant species. These recommendations are:

(1) Individuals should be removed with as little physical disturbance as possible to the individual, and at a phenologically appropriate time of year, as when the individual is dormant or photosynthetically inactive;

(2) The receptor site should be of the same habitat quality, particularly with respect to soil type and its physical characteristics. Various other manipulation aspects of the receptor site may include weeding to decrease competition from native and exotic species, watering during times of drought, and fencing and/or other forms of site protection; and

(3) Knowledge of the biology of the organism appears to aid greatly in the design of appropriate horticultural techniques for the preparation of cuttings, transplantation, seed germination, *etc*. This is problematic, however, because the biology of most State-listed species is poorly known. Although some species such as cacti and succulents may be amenable to standard horticultural techniques for propagation, most are not. Therefore, without sufficient knowledge of the biology of impacted species, success of the transplantation, relocation, or reintroduction will not be assured.

Finally, it is suggested that because of the lack of or limited success (21; 32% combined) of most of the transplantation, reintroduction, or restoration attempts documented, and the uncertainty of many of the on-going projects, the Endangered Plant Program of the California Department of Fish and Game's Natural Heritage Division should remain extremely cautious in any mitigation agreement that will allow any of these techniques to serve as mitigation for project impacts.

TABLE OF CONTENTS

LIST OF TABLES

II. INTRODUCTION AND PROJECT OBJECTIVES

The Endangered Plant Program (EPP) of the California Department of Fish and Game (CDFG) requested that mitigation-related transplantation, relocation, and reintroduction projects involving the State's endangered, threatened, and rare plant species be assessed for overall project efficacy and success. Thus the purpose of this research is to document the results of mitigation-related projects of this type involving the State's rare plant species of concern. The documentation may serve in the future as a position paper for the EPP's policy on transplantation, relocation, and reintroduction of State-listed species as mitigation.

The Department of Fish and Game currently requires an approved Mitigation Agreement (MA) for the manipulation of State-listed species (*cf.* Howald and Wickenheiser 1990). An MA is the legal document used by CDFG to approve mitigation projects for State-listed species that are required under the California Environmental Quality Act, Statutes, and Guidelines (CEQA). Mitigation is not explicitly defined in CEQA, but is listed as "including":

(a) Avoiding the impact altogether by not taking a certain action or parts of an action.

(b) Minimizing impacts by limiting the degree or magnitude of the action and its implementation.

(c) Rectifying the impact by repairing, rehabilitating, or restoring the impacted environment.

(d) Reducing or eliminating the impact over time by preservation and maintenance operations during the life of the action.

(e) compensating for the impact by replacing or providing substitute resources or environments (CEQA §15370).

If these five forms of mitigation are interpreted as priority in order of listing, then the preferred form of mitigation under CEQA (1986) is project avoidance, followed by minimization of impacts, rectification of impacts, *etc.* It should be noted that compensation is the least preferable form of mitigation under this interpretation.

III. METHODS

Questionnaire: To begin the assessment, a questionnaire was developed by the author and reviewed by members of the CDFG's Endangered Plant Program. Three hundred seventy-seven (377) individual questionnaires were sent in the summer of 1989, along with, at that time, a current list of State-listed endangered, threatened, and rare plant species (California Department of Fish and Game 1989), to a broad spectrum of public resource and land management agencies, consulting firms, nurseries, museums, academic institutions, and private individuals or conservation organizations (Table 1). The individuals selected for the survey were compiled from California Native Plant Society and California Department of Fish and Game files, and personal mailing lists. The questionnaire and cover letter are included as Appendix A. The mailing list is included as Appendix B.

Review of Internal Files: Project and species files held by the EPP were reviewed in the winter of 1990, to clarify materials received from the questionnaire and to gather additional information. These files were particularly helpful regarding the MOU and MA conditions of the mitigation-related projects. Most, but not all of the current (*i.e.*, on-going and/or currently negotiated) mitigation-related transplantation, relocation, and reintroduction projects were reviewed. However, several recently initiated and on-going projects that conform to newly instituted EPP mitigation standards are not reviewed in this document because assessment of their success is not possible at this time.

Mitigation Project Assessment: The questionnaires received and EPP files reviewed were examined for the following information:

(1) whether the project reported was mitigation- or research-related,

(2) mitigation project objective(s),

(3) responsible party's criteria for mitigation success,

(4) transplantation, relocation, or reintroduction methods,

(5) design and implementation of the mitigated population's monitoring plan,

(6) respondent's assessment of mitigation project success, and

(7) date of transplantation, reintroduction, or relocation project.

Once these data were compiled, the projects were tallied for their assessed success and efficacy. The results of this analysis are summarized in Section IV.

IV. RESULTS

A total of one hundred sixty-eight (168) questionnaires was returned for this survey. All those organizations and individuals who responded to the questionnaire, and their summary responses are listed in Appendix C.

The majority of respondents (114, 68%) have not been involved in any transplantation, relocation, or reintroduction project involving state- (or federally-) listed endangered, threatened, or rare plant species. Twenty-four (24) individuals have been involved, however, and they are reviewed in detail in Section IV.A and IV.B. Table 2 outlines the responses to questionnaire.

A significant number of respondents reported on transplantation, relocation, and reintroduction projects that were not mitigation-related, but rather, research-related. Mitigation-related projects are defined as those that required either an MA or formerly, a Memorandum of Understanding (MOU). Thus several of the projects described in the returned questionnaires were research activities that did not require a Mitigation Agreement (MA). These projects were included in the analysis, and are described in Section IV.B. However, the listing is not exhaustive for research-

TABLE 1. SUMMARY OF RECIPIENTS OF THE MITIGATION QUESTIONNAIRE

Organization or Individual	Number[1]
Consulting Firms	66
Resource Agencies	
Federal	9 (30)[2]
State	10 (43)[3]
County	10 (15)[4]
City	3[5]
Private Nature Preserves	7
Museums	7
Private Energy Companies	1
Public Utilities	4
Private Conservation Organizations	4
Botanic Gardens	6
Nurseries	4
Universities	20 (29)[6]

[1]The number of questionnaires will not sum to a total of 377 because in many cases several individuals within the same office were sent a questionnaire. Therefore, although the questionnaire may have been duplicated within any one office, the probability of receiving a response was increased.

[2]The first number in this column represent the total number of different federal agencies queried. These included the U.S. Fish and Wildlife Service, U.S. National Park Service, U.S. Environmental Protection Agency, U.S. Army Corps of Engineers, U.S. Bureau of Land Management, U.S. Soil Conservation Service, U.S. Air Force, U.S. Navy, and the U.S. Forest Service. The number in parentheses indicates the total number of federal agency offices contacted.

[3]The first number in this column represents the total number of different state resource agencies queried. These included the California Department of Fish and Game, Department of Forestry, Department of Transportation, Jackson State Forest, State Lands Commission, California Conservation Corps, California Department of Parks and Recreation, Department of Water Resources, Department of Food and Agriculture, and the Division of Mines and Geology.
The number in parentheses indicates the total number of state offices contacted.

[4]The first number represents the total number of county offices queried. These include planning and resource offices in the following ten counties: Chico, Placer, San Diego, San Luis Obispo, Sacramento, Santa Barbara, Solano, Sonoma, Tuolumne, and Yolo. The number in parentheses represents the total number of county offices contacted.

[5]Planning and resource agencies were contacted in the cities of Santa Rosa, Modesto, and San Diego.

[6]The first number in this column represents the total number of different colleges and universities queried, including American River College; Butte College; California Polytechnic Pomona; California State Universities at Bakersfield, Chico, Hayward, Humbolt, Sacramento, San Diego, San Francisco, San Jose, and San Luis Obispo; Mills College; Pacific Union College; Palomar College; Stanford University; University of California at Berkeley, Davis, Santa Barbara, and University of San Diego.

TABLE 2. SUMMARY OF RESPONSES TO MITIGATION QUESTIONNAIRE

Organization	Number of Questionnaires Sent	Responded Yes	Responded No[7]
Private Individuals/			
Citizen Groups	90	2	24
Consulting Firms	66	6	18
Resource Agencies			
State Agency Offices	10 (44)[8]	11	9
Federal Agency Offices	9 (30)	7	13
County Offices	10 (15)	4	9
City			
University Faculty	20 (29)	5	11
Museums	7	0	3
Private Nature Preserves	7	0	3
Botanic Gardens	6	1	2
Nurseries	4	1	1
Public Utilities	4	0	3
Private Conservation Organizations	4	0	1

[7]In all cases in this table, the total number of respondents will not total to 168 because multiple individuals were contacted within a single office or agency, and therefore multiple questionnaires were returned from a single office or agency.

[8]In all cases, first number in the column represents the total number of agencies queried, and the number in parentheses represents the total number of offices contacted.

related transplantation, relocation, and reintroduction projects, but it is considered nearly so for completed mitigation-related projects of these types.

A total of forty-six (46) projects were review, involving 53 transplantation, relocation, or reintroduction efforts. Forty (40) plant species were reviewed, 34 (85%) are listed by the State, federal goverment, or the California Native Plant Society as either endangered, threatened, or rare. Specifically, 25 (63%) are listed by the State as endangered, 3 (8%) are listed asthreatened, and 6 (15%) are listed as rare, and 6 (15%) are not listed by the State, but have some other form of protection or special status (California Department of Fish and Game 1990, Smith and Berg 1988).

In addition, the 40 plant species reviewed belonged to 21 plant families. Asteraceae represented the highest number of species involved (9; 23%) including species in the genera *Blennosperma, Cirsium, Eriophyllum, Hemizonia, Lasthenia*, and *Pentachaeta*. This was followed by the Brassicaceae (4; 10%), encompassing the genera *Arabis, Eryngium*, and *Erysimum*. Eight additional plant families were represented by two taxa, while ten families were represented in this study by one taxon. The genus *Erysimum* had the greatest number of taxa (3) involved in this study, followed by the genera *Brodiaea, Hemizonia, Lupinus*, and *Oenothera* (2 each).

Additional results of the survey indicate that of the 46 projects reviewed, 38 (83%) are mitigation-related, while eight (17%) are research-related. Of the 53 manipulation attempts, forty-one (41; 77%) involved translocation (including relocation) of species of concern, nine (9) projects (17%) involved reintroduction, and 2 projects (4%) involved restoration of a population of a State-listed species. One additional project reviewed is a research-related project that has yet to include a transplantation, relocation or restoration component.

Of the 46 projects reviewed, 40 projects have been implemented, while 4 projects are in the planning stages. Of the total 46 projects, only 15 projects (33%) had explicitly defined criteria for success of the mitigation project, while the remaining 31 projects (67%) either had not criteria for success or the criteria were only vaguely defined.

Only 15% (8) of the 53 transplantation, relocation, or reintroduction attempts reviewed should be considered fully successful (13% of the 46 projects). I define "success" in this survey as either: (1) the respondent to the questionnaire felt that the project was successful; or, (2) greater than 75% of the mitigation propagules established a reproducing population over the life of the project as reported. "Unsuccessful" projects were determined to be so in this survey because either: (1) the respondent in the questionnaire reported that the project was unsuccessful; or, (2) less than 25% of the mitigation propagules established a population, and subsequently died. "Limited success" was assigned to those projects for which: (1) the respondent in the questionnaire reported as "limited" or "partially" successful; or, (2) the respondent reported a middle range of mitigation propagule establishment (>25% but <75%).

Plant species for which the transplantation, relocation, or reintroduction project was successful included *Amsinckia grandiflora, Dudley cymosa* ssp. *marcescens, Holocarpha macradenia, Lasthenia burkei* (3 projects), *Opuntia basilaris* var. *treleasei*, and *Sidalcea pedata*. However, of the eight projects involving these species, only four are mitigation-related; therefore the success rate of the mitigation-related attempts is 8%. An additional seven (7) transplantation attempts (13%) are considered partially successful, or of limited success. Twelve (12) of the 53 attempts (23%) are considered here to be unsuccessful, and the success of an additional four projects is unknown (*i.e.*, unreported or no information was found in EPP files). Sixteen projects (35%) could not be evaluated for their success because they are on-going or in the planning stages.

IV.A. Rare, Threatened and Endangered Plant Species Involved in Mitigation-Related Transplantation, Relocation and Reintroduction Projects

The following is a discussion of the state- (and federally-) listed species that have been the subject of mitigation-related transplantation, relocation and reintroduction projects, as outlined by the respondents of the questionnaire and a review of the EPP files. Table 3 lists the endangered, threatened and rare plant species involved in transplantation, relocation, and reintroduction projects. Information from the questionnaire and EPP files is summarized briefly by species. Questionnaires and personal notes are on file and available for review of additional information.

IV.A.1. *Acanthomintha ilicifolia* (San Diego Thornmint): State endangered; Federally Candidate Category 1, CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: "Westview Planned Residential Development." The Pardee Company agreed to mitigate for destruction of a population of *A. ilicifolia* by the construction of a road (Black Mountain Road) and a housing development by creating a 13.6 acre on-site open space preserve for the San Diego thorn-mint.

Mitigation-Related?: Yes.

Project Objectives: The goal of the mitigation plan was to create a viable population of *A. ilicifolia* in an on-site preserve through the importation of seed and soil.

Project Methods: The Pardee Company contracted with Environmental and Energy Services Company (ERC) to salvage all the *Acanthomintha ilicifolia* seeds in the population affected by the construction. Approximately 10.8 gm. of seed were collected in July 1988. Topsoil was then salvaged from the *Acanthominta ilicifolia* population area to collect seed potentially stored in the soil. The soil was transported to the mitigation site.

TABLE 3. **CALIFORNIA STATE ENDANGERED, THREATENED, AND RARE PLANT SPECIES INVOLVED IN MITIGATION-RELATED OR RESEARCH-RELATED TRANSPLANTATION, RELOCATION, OR REINTRODUCTION PROJECTS**

SPECIES	FAMILY	PROTECTION STATUS[9]
Acanthomintha ilicifolia	Lamiaceae	Endangered
Amsinckia grandiflora	Boraginaceae	Endangered
Antennaria flagellaris	Caryophyllaceae	None
Arabis macdonaldiana	Brassicaceae	Endangered
Arctostaphylos hookeri var. *ravenii*	Ericaceae	Endangered
Bensoniella oregana	Saxifragaceae	Rare
Blennosperma bakeri	Asteraceae	Rare
Brodiaea filifolia	Amaryllidaceae	Endangered
Brodiaea insignis	Amaryllidaceae	Endangered
Calochortus greenei	Liliaceae	None (Fed C2)
Chorizanthe howellii	Polygonaceae	Threatened
Cirsium occidentale var. *compactum*	Asteraceae	None (Fed C2)
Cordylanthus palmatus	Scrophulariaceae	Endangered
Croton wigginsii	Euphorbiaceae	Rare
Dudley cymosa ssp. *marcescens*	Crassulaceae	Rare
Eriastrum densifolium ssp. *sanctorum*	Polemoniaceae	Endangered
Eriophyllum mohavense	Asteraceae	None (Fed C2)
Eryngium aristulatum var. *parishii*	Apiaceae	Endangered
Erysimum capitatum var. *angustatum*	Brassicaceae	Endangered
Erysimum menziesii	Brassicaceae	Endangered
Erysimum teretifolium	Brassicaceae	Endangered
Gilia tenuiflora ssp. *arenaria*	Polemoniaceae	Threatened
Hemizonia increscens ssp. *villosa*	Asteraceae	Endangered
Hemizonia minthornii	Asteraceae	Rare
Holocarpha macradenia	Asteraceae	Endangered
Lasthenia burkei	Asteraceae	Endangered
Lilaeopsis masonii	Apiaceae	Rare
Lupinus tidestromii var. *tidestromii*	Fabaceae	Endangered
Lupinus milo-bakeri	Fabaceae	Threatened
Mahonia nevinii	Berberidaceae	Endangered
Monardella linoides ssp. *viminea*	Lamiaceae	Endangered
Oenothera deltoides ssp. *howellii*	Onagraceae	Endangered
Oenothera wolfii	Onagraceae	None (Fed C2)
Opuntia basilaris var. *treleasei*	Cactaceae	Endangered
Orcuttia viscida	Poaceae	Endangered
Pentachaeta lyonii	Asteraceae	Endangered
Pogogyne abramsii	Scrophulariaceae	Endangered
Pseudobahia peirsonii	Asteraceae	Endangered
Sedum albomarginatum	Crassulaceae	None (Fed C1)
Sidalcea pedata	Malvaceae	Endangered

[9]State of California, Department of Fish and Game, Nongame-Heritage Program, Endangered Plant Project. Designated Endangered, Threatened or Rare Plants. 1990.

Twenty-five (25) 4 ft^2 experimental plots in the preserve were located and prepared by removing existing vegetation. Seeds sown in the test plots were observed in December, 1988, while the remaining seed was sent to the Rancho Santa Ana Botanic Garden (RSA) for germination tests.

Seedlings occurred in 12 of the 25 test plots in March 1989. At the time of the preparation of this report, no additional information is available. However, the MOU on file requires a monitoring program to be established in the mitigation plots that must continue for five (5) growing seasons.

Criteria for Success: As outlined by the MOU, performance criteria include: (1) erosion control [soil stabilized]; (2) weed invasion [no interference with *A. ilicifolia* establishment]; (3) herbivory ["minimal" damage to *A. ilicifolia* seedlings]; (4) vigor [5 cm minimum height per individual plant]; and, (5) reproductive success [to be determined on the basis of offsite monitoring].

Project Success: Project on-going.

Date Project Initiated: July 1988.

2) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Shea Homes Palos Vista Development." Shea Homes designed a development of 979 acres within the city of Escondido that involved the construction of 730 homes and some open space. Shea Homes contracted initially (October 1988) with Royce B. Riggins and Associates (RBR), working in conjunction with Mr. Jim Dillane of the Lake Hodges Native Plant Club, to prepare the biological reports and initial mitigation design for the project. In May, 1989, ERC completed the work initiated by RBR. The mitigation site was selected as the San Diego Wild Animal Park.

Mitigation-Related?: Yes.

Project Objectives: The goal of the mitigation contract was to assure the preservation of two small disjunct populations of *Acanthomintha ilicifolia* that were originally located within the boundaries of the Palos Vista residential development.

Project Methods: Plants were collected in June and July of 1988 and transplanted to the mitigation site. The site is a 40 x 30 ft parcel on which a 2 ft layer of subsoil was imported and laid down prior to transplantation.

Criteria for Success: As outlined by the MOU on file, performance criteria are based on reproductive success, as follows: (1) number of plants shall equal or exceed 30% of the mean density of plants in natural populations at the first end of the growing season; (2) number of plants shall equal or exceed 50% of the mean density of plants in natural populations at the end of the second growing season; (3) number of plants shall equal or exceed 70% of the mean density of plants in natural populations at the end of the third growing season; (4) number of plants shall equal or exceed 90% of the mean density of plants in natural populations at the end of the fourth growing season; and, (5) number of plants shall equal or exceed 100% of the mean density of plants in natural populations at the end of the fifth growing season.

Project Success: Project on-going.

Date Project Initiated: December 1988.

3) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Reparation for the Sabre Springs Development." One of the largest known populations of *Acanthomintha ilicifolia* is located on property located within the City of San Diego Open Space System, previously owned by the Pardee Company. In the spring of 1989, the population was reduced by one-third due to an accidental road grading operation. In order to avoid prosecution by the State for these damages, Pardee Company was notified of several measures to rectify the damage. Pardee Company has or is complying with all seven conditions of the reparation plan, but with varying degrees of success.

Mitigation-Related?: Yes.

Project Objectives: To rectify the accidental damage inflicted on a large population of *Acanthomintha ilicifolia*

Project Methods: The disturbed population was fenced and bermed, signed, weeded, and the adjacent roadbed hydroseeded. A second phase of the project will be to manage suitable *Acanthomintha ilicifolia* areas near existing populations to encourage their spread. Seed will be broadcast onto suitable clay soils adjacent to extant stands in January, 1992.

Criteria for Success: As stated in the reparation plan, the goal of the project is to increase the remaining *Acanthomintha ilicifolia* population to predisturbance size or greater.

Project Success: Project on-going.

Date Project Initiated: Spring-summer 1989.

4) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Indian Hill," "McIntire" ("Las Brisas"), and "Spyglass" urban development projects. The three projects together required translocation of *Acanthomintha ilicifolia* to open space areas on the development sites. Mitigation projects were contracted to Pacific Southwest Biological Services (PSBS) of San Diego. PSBS was responsible for all relocation activities, including seed collection, and excavation and placement of clay soils associated with *Acanthomintha ilicifolia* (PSBS, Inc. 1988).

Mitigation-Related?: Yes.

Project Objectives: None stated. Presumably the project objectives were to establish viable populations of *Acanthomintha ilicifolia* from transplanted plant material at four translocation sites (open space areas onsite at the Las Brisas and Indian Hill sites; within a natural, dedicated open space area at the El Camino Condominium and Tennis Club; a project adjacent to the Spyglass project; and within the natural area of the Quail Botanical Garden

County Park.

Project Methods: Seeds were collected at Jetton Property (Las Brisas Mobile Home Park) during the summer of 1986 and sewn by hand on the relocated clay lens. Soils were excavated and prepared for seeding within a 24-hour period. Seeds were collected as whole plant material, occupying approximately 1/2 yd^3 and weighing about 2 pounds.

Criteria for Success: None state specifically.

Project Success: The project was halted and the MOU terminated due to the difficulty the EPP had in dealing with PSBS. Success of the transplantation was limited as of May 1988. However, at the Las Brisas relocation site in May 1988, an estimate of between 700-1000 individuals (1100 "flowering heads") was reported. At the Quail Gardens relocation site, the population estimate was made during the seedling stage. As of 8 May 1988, "seed heads" numbered 70, while the population survey during the seedling stage resulted in 200-300 plants. PSBS reported that associated native plant species were abundant at the Las Brisas site, though more rare at Quail Gardens.

Date Project Initiated: Spring 1985

IV.A.2. *Blennosperma bakeri* (Sonoma Sunshine): Not state listed; Federal Candidate C2; CNPS List 1B.

1) Respondent: Mr. Charlie Patterson, Plant Ecologist. Private Consultant, El Cerrito.

Project Name and Description: "Montclair Park." Project involved the construction of a small housing development by Christopherson Homes in the city of Sonoma (lead agency for the permit). entitled "Montclair Park." The mitigation included the dedication (as compensation) of approximately 2.0 acres of undeveloped land, located on the edge of the development, within which up to 1.0 acres of actual vernal pool habitat would be created and seeded with *Blennosperma bakeri* and associated vernal pool species.

Mitigation-Related?: Yes.

Project Objectives: Objectives for the housing development were the replacement of 0.3 to 0.5 acres of wetlands and of the pre-existing 10,000 individuals of *Blennosperma bakeri* that were destroyed during the construction of the housing development.

Project Methods: The habitat was graded and shaped, creating approximately 10 new vernal pools in a soil that is underlain by the same clayplan existing under the destroyed pools.

Blennosperma bakeri seeds were collected in late May 1989 by collecting the dry flower heads, vacuuming the surface for seeds, duff and dust, and scraping by hoe, 1-2 inches of the top soil of existing pools. Collected seed and duff was air-dried in shallow trays in a cool, dry environment. Seeds were transferred to the created pools by hand. The created pools were fenced (wood and wire) and a berm constructed for protection.

The project design also included several additional trial vernal pools within a storm runoff detention basin to investigate the feasibility of managing detention basins and vernal pools concurrently as a contaminant settling basin.

Monitoring of the pools includes: (1) habitat integrity and stability; (2) *Blennosperma bakeri* growth and reproduction; and, (3) overall vernal pool community development.

Criteria for Success: Essentially the replacement of a self-sustaining colony of *Blennosperma bakeri*. This includes: (1) at least 75% of the created vernal pool habitat should be documented as stable, with no measurable erosion or deposition, and with no significant channel formation; (2) at least 75% of the pools should have adequate [undefined] water-holding capacity; (3) local drainage patterns should be shown to be adequate [undefined] to fill the pools (75%) without input from street runoff or eucalyptus debris; (4) at least 10 colonies of *B. bakeri* should be established in the new pools, and be self-sustaining populations; (5) the total habitat area of at least 0.3 acres should be dominated by *Blennosperma bakeri* for at least 2 years without supplement seeding; (6) the total population should number at least 10,000 individuals without supplemental seed over 2 years; (7) at least 75% of the total pool habitat should be dominated by typical (native?) vernal pool plants; (8) each pool should contain at least 4 (native?) vernal pool species; and, (9) encroachment by grasses and/or upland weeds should be documented as stable, with no significant advancement into the pools over the last 2 years of the monitoring program.

Project Success: Respondent felt that, after one dry year, the results are promising -- *i.e.*, several thousand individuals of *Blennosperma bakeri* are established. However, the pools need to be regraded and probably deepened.

Date Project Initiated: 1989.

2) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Santa Rosa Rare Plants Mitigation Plan San Miguel Estates 1." In 1989 Cobblestone Development Corporation proposed the development of San Miguel Rancho Subdivision (RSM) at 2001 Waltzer Road within the city of Santa Rosa, Sonoma County and San Miguel Estates No. 2 (SME) at 2192 Francisco Avenue, also within Santa Rosa. The SME project is an on-going housing construction and the RSM housing project was a 1989 development. The projects would destroy approximately 2.51 acres of vernal pool habitat. (see IV.A.19(3) for more details.)

Mitigation-Related?: Yes.

Project Objectives: According to the Mitigation Agreement between Cobblestone and CDFG, the mitigation should establish self-sustaining populations of plants in approximately 2.97 acres of newly created habitat on the mitigation site. Self-sustaining is defined as approximately 13,000 individuals of *Lasthenia burkei* and 137,000 individuals of *Blennosperma bakeri* for 2 consecutive years without supplemental seeding.

Project Methods: The mitigation plan was devised by R. Osterling, Inc. (1989). The plan proposed to transplant all existing plants and/or seeds to a 20-acre receptor site located approximately 1.5 miles west of the San Miguel Estates property, with existing 3.49 acres of vernal pool resources. Approximately 2.5 acres of vernal pool habitat will be constructed at the receptor site with pool configuration and depth based on survey of existing pools. Grading will be done with small equipment under supervision of a qualified botanist (Charlie Patterson, private consultant). Plant material will be "transferred." Seed will be collected from donor pools and the top 1-2 inches of pool bottom duff will be excavated and spread in the excavated pools at the receptor site. Monitoring will continue through June 1991.

Criteria for Success: None explicitly stated.

Project Success: Unknown. No information found in EPP files.

Date Project Initiated: March 1989.

IV.A.3. *Brodiaea filifolia* (Thread-leaved Brodiaea): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: "College Area Specific Plan in San Marcos." The Baldwin Company proposed a development on 530 acres of undeveloped land in the City of San Marcos, on a ridge behind the college. The onsite population of *Brodiaea filifolia* is part of the county's most extensive, known population.

According to the monitoring plan (WESTEC 1988), the mitigation plan included: (1) all onsite mitigation activities; (2) a 12-acre preserve that is completely fenced (vinyl-clad chain-link), protected for the life of the project; (3) planting of (presumably) local plants; (4) creation of a stable, relatively weed free *Brodiaea filifolia* population, requiring low maintenance; (5) onsite salvage of each plant species included in the preserve; (6) transportation and laying of suitable soils (Huerhuero Series); (7) maintenance during the first several years; and, (8) monitoring by a qualified botanist.

Mitigation-Related?: Yes.

Project Objectives: Two objectives were identified: (1) to set aside a 12-acre preserve for existing native grassland habitat supporting *B. filifolia*; and, (2) to reintroduce *Stipa pulchra* (purple needle grass) to disturbed portions of the preserve (ERC Environmental and Energy Services Co. 1990c).

Project Methods: During 1988, clay soils and 8167 *B. filifolia* corms were collected from a 25 ft^2 area within the original population and brought to the preserve. Five plots were marked and rabbit exclosures were installed. The largest corms collected were planted in planting holes in the test plots and throughout the preserve. Smaller corms were shipped to a contract nursery (Tree of Life Nursery, San Juan Capistrano) to be grown for increased size. A portion of these corms (870) were outplanted in the fall of 1990. Seed of *Brodiaea filifolia* also was collected from the original population and seedlings were grown at the nursery for two seasons. These were planted in the preserve in 1990 (ERC Environmental and Energy Co. 1990c).

Monitoring includes: (1) overall success; (2) role of corm size in relation to survivorship and flowering; (3) field establishment of nursery corms under controlled conditions with and without fertilizer treatments; (4) efficacy of relocating *B. filifolia* populations by soil importation; (5) role of supplemental irrigation in the establishment of transplanted corms; and, (6) use of field-collected seed and nursery-generated seedling corms in restoration (ERC Environmental and Energy Services Co. 1990c).

Criteria for Success: Criteria for success includes: (1) 75% survival rate of *Brodiaea filifolia* corms in test plots and 80% in the grassland; (2) 80% survival rate of *Stipa pulchra* plugs (seeds were planted similarly and an 80% survival rate was considered for this activity); (3) weeds should not cover the test plots dense enough to interfere with *Brodiaea filifolia* establishment and noxious weed species [undefined] should be eliminated from the preserve. The same criteria were considered for the *S. pulchra* plantings; (4) herbivory damage assessed as above-ground and below-ground growth for *B. filifolia*. Acceptable damage to vegetative material is 10% or less of all plantings. Gopher damage to corms cannot exceed 5% in any one plot or 20% overall; and, (5) acceptable herbivory losses for *S. pulchra* should not exceed 10%. No criteria were established for reproductive success, "offset" production of corms, or soil importation.

Project Success: Project is in-progress and will continue until December 1993. To date, preliminary results of the monitoring efforts indicate that the introduction of *Brodiaea filifolia* corms has been largely successful. Corm growth increased significantly between 1989 and 1990. Eighty-seven percent (87%) of the corms have remained viable and 19.9% have produced "offsets." Also, fertilizer treatments of corms grown in the nursery did not improve vegetative development. Irrigation showed initial signs of promise in improvement of establishment of corms, particularly with soil importation. At the time of the monitoring report, results were not available for assessing the success of the transplanted nursery-grown corms. Direct seeding was not successful, in either the irrigated or non-irrigated seed locations. Why it was not successful is not known, but it may be possible that the seeds were held in storage too long and lost viability.

The 1989 planting of *Stipa pulchra* plugs was not successful due to the late planting in conjunction with very warm weather and drought. A portion of the plugs was replaced in winter 1990, and an additional experimental plot was installed in 1990 to test the effects of supplemental irrigation on *S. pulchra* establishment. Significantly more plants survived than those grown from seed (94.8% *vs.* 61.6%).

Efforts to eliminate sweet fennel (*Foeniculum vulgare*) and cardoon (*Cynara carduncului*) have largely been successful, although mustard (*Brassica* [*nigra?*]), wild radish (*Raphanus sativus*), and invasive annual grasses are not controlled.

Herbivory on *Brodiaea filifolia* by rabbits does not appear to be a problem, although there appears to be some disturbance by gophers within as well as outside the exclosures (ERC Environmental and Energy Services Co. 1990c).

Date Project Initiated: May 1988.

IV.A.4. *Brodiaea insignis* (Kaweah Brodiaea): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: Mr. John Stebbins, Fresno.

Project Name and Description: "Kaweah Reservoir Dam Expansion" (Tulare County), initiated by the California Department of Water Resources. Project plans are being drafted at this time.

Mitigation-Related?: Yes.

Project Objectives: Project plans are being drafted at this time. Net yet available.

Project Methods: Project plans are being drafted at this time. Net yet available.

Criteria for Success: Project plans are being drafted at this time. Net yet available.

Project Success: Net yet available.

Date Project Initiated: 1989.

IV.A.5. *Calochortus greenei* (Greene's Mariposa Lily): Not state listed; Federal Candidate C2; CNPS List 1B.

Respondent: Mr. William Ferlatte, Siskiyou County Dept. Agriculture and Ms. Barbara Williams, U.S. Forest Service, Klamath National Forest.

Project Name and Description: None. *Calochortus greenei* is not a state-listed species, and both respondents answered briefly. Project involved a road widening/construction project that required two mitigation transplantation efforts.

Mitigation-Related?: Yes.

Project Objectives: None stated.

Project Methods: None stated, but presumably the bulbs were dug by hand and transported to the mitigation sites and replanted there.

Criteria for Success: None stated.

Project Success: Approximately 65 plants/bulbs were transplanted on May 23, 1989. As of May 9, 1990 [sic] (June 1989?), approximately 10 individuals survived the transplantation onto U.S. Bureau of Land Management and private property. This resulted in a survivorship rate of approximately 15%.

Date Project Initiated: May 1989.

IV.A.6. *Chorizanthe howellii* (Howell's Spineflower): State threatened; Federal Candidate C2; CNPS List 1B.

Respondent: Ms. Frederica Bowcutt, State of California Department of Parks & Recreation, Sacramento.

Project Name and Description: None. Project involved the reintroduction of *Chorizanthe howellii* and *Erysimum menziesii* to archeological sites at MacKerricher State Park (Mendocino County) after an archeological dig. The site is a coastal dune ecosystem. University of California, Davis, initiated an archeological dig in 1989-90 at sites containing rare species. (see IV.A.13(1) for more details).

Mitigation-Related?: Yes.

Project Objectives: None stated.

Project Methods: Seed was collected in the summer of 1989 from the plants on site before the archeological dig was initiated. Plug plants were grown at the California Conservation Corps (CCC) Napa nursery and outplanted in February 1990 by the CCC. Plants were monitored by an undescribed photo monitoring technique. Outplanted plants also were counted and mapped. Initial costs for the project were: (1) salary $800.00; (2) travel $400.00; and, (3) plants $200.00, for a total of $1400.00.

Criteria for Success: None stated.

Project Success: Project on-going. Information not yet available.

Date Project Initiated: July 1989.

IV.A.7. *Cirsium occidentale* var. *compactum* (Compact Cobweb Thistle): Not State listed; Federal Candidate C2; CNPS List 1B.

Respondent: Mr. Gary Ruggerone, California Department of Transportation, San Luis Obispo.

Project Name and Description: California Department of Transportation is involved in two projects, "Little Pico Bridge Replacement" and "Piedras Blancas Shoulder Widening." The former is on-going, and the latter was conducted in 1986. Both projects are along Highway 1 in San Luis Obispo County on ocean bluffs. *Cirsium occidentale* var. *compactum* is found along the disturbed highway shoulders.

Mitigation-Related?: Yes. However, neither project included CEQA permit conditions regarding transplantation of *Cirsium occidentale* var. *compactum*, although California Department of Transportation consulted with the USFWS.

Project Objectives: Transplantation and reseeding of the disturbed areas with *Circium occidentale* var. *compactum* to maintain populations.

Project Methods: Plants of various ages were removed from the impact area and were transplanted to immediately adjacent areas in January and February (1987?). Seed was collected in July through October (1986?), scarified, and scattered in January and February (1987?).

Both sites are monitored several times per year until it can be determined whether a reproducing population has been established. Neither site has received long-term protection, although the areas are considered by Caltrans as "environmental sensitive areas." Costs of the projects have been absorbed in the overhead. No reports other than brief field notes of the transplantation were filed.

Criteria for Success: Success was defined as survival of transplants and germination of seed for reintroduction to establish a continued presence of *Cirsium occidentale* var. *compactum* in the area.

Project Success: For Piedras Blancas, there was only partial success. Transplanting was a total failure, but the respondent reported some success with reseeding. For Little Pico, the transplantation was a failure. Seeding has not yet been initiated.

Date Project Initiated: 1986.

IV.A.8. *Croton wigginsii* (Wiggin's Croton): State rare; Federal Candidate C3C; CNPS List 2.

Respondent: Mr. Gerald Hillier, U.S. Bureau of Land Management, Riverside.

Project Name and Description: None. Project involved the construction of a new campsite ("Gecko") at the Imperial Sand Dunes, immediately south of Highway 78 (Imperial County).

Mitigation-Related?: Yes.

Project Objectives: Objectives were to establish seedings of *Croton wigginsii* in an adjacent Wilderness Study Area (WSA).

Project Methods: Seedlings were dug with a shovel of sand, and then placed in a bucket of wet sand. The buckets were transported approximately 1 mile away to a WSA site on the north side of Highway 78. A slice with a shovel was made in the new substrate, and the seedlings were transplanted in approximately 5 per group. About 12 groups were established.

The seedlings were visited approximately every three days for two weeks to monitor the success of the transplantation. During that two-week period, all the seedlings died.

Criteria for Success: Not clearly stated. Respondent suggested that the criterion was successful establishment of transplanted seedlings.

Project Success: Respondent considered that the project was successful because it established whether transplantation of *C. wigginsii* seedlings would be a viable option. However, as stated above, none of the seedlings survived and therefore, it should not be considered successful from a biological viewpoint.

Date Project Initiated: Unknown.

IV.A.9. *Eriastrum densifolium* ssp. *sanctorum* (Santa Ana River Woollystar): State endangered; Federal endangered; CNPS List 1B.

Respondent: Mr. Craig Martz, Associate Environmental Planner, California Department of Transportation, Sacramento, and data obtained from EPP files.

Project Name and Description: "Santa Ana River Woollystar Relocation Project." California Department of Transportation (Caltrans) attempted to change State Route 30 in San Bernadino County. The project included freeway construction along State Route 30, and a second phase of construction between Interstate 10 in Redlands and Fifth Street in the City of San Bernadino. Grading in the second phase would have resulted in the loss of approximately 1.24 acres of alluvial scrubland, habitat for 1039 individuals of *Eriastrum densifolium* ssp. *sanctorum*. However, the project was modified to affect only 733 individuals, with the remaining 308 individuals preserved in a designated environmental sensitive area avoided during the construction phase. The area is to be protected in perpetuity once construction is completed.

Mitigation-Related?: Yes.

Project Objectives: None stated specifically, but the overall objective appears to be the successful establishment of transplanted individuals of *Eriastrum densifolium* ssp. *sanctorum* from along State Route 30 in the Santa Ana River Wash to three transplant receptor areas within the right-of-way.

Project Methods: A contractor (Nativescapes) was hired to transplant 733 individuals of *E. densifolium* ssp. *sanctorum* from the west side of the Highway 30 project site to three locations on the east side of the highway, during January through March 1988. Plants were removed with a Vermeer TS-20 tree spade mounted on a Bobcat tractor. Plants were then fitted into burlap-lined mesh baskets that conformed to the rootballs for transport to the recipient areas. Individuals were planted in rows within each of the three transplant areas. Each row as initially marked with a wooden stake that was labeled with the number of individuals in the row. However, this labeling method was deemed inadequate in the second year of monitoring. Transplants were then marked individually with aluminum tags. Monitoring of the transplants is to be conducted for three years following the transplantation.

Criteria for Success: None stated explicitly.

Project Success: Respondent felt that the project had not achieved the level of success that was hoped for, in part because of the current drought conditions. After the first year of monitoring, Transplant Area 1 suffered a 39% mortality, Transplant Area 2 suffered a 56% mortality, and Transplant Area 3 suffered a 48% mortality of transplants. Most of the mortality in the first year was attributed to transplant shock, although natural mortality and competition may also be responsible in part (Martz 1990). The first year monitoring report suggests that the transplantation project was "highly successful thus far" because of relatively high survivability (61%, 44%, and 52% in Areas 1, 2, and 3, respectively), and good seedling production was observed.

Results of the May 1990 monitoring (Martz 1990) indicate a survival rate of 46.7% in Transplant Area 1, 38.9% in Transplant Area 2, and 40.5% in Transplant Area 3. The overall survival for the three areas was 332 individuals (44.2%). Approximately 85.5 percent of the surviving individuals were reproductive; however, 31 individuals (9.3%) were considered to be in obvious decline.

Seedling recruitment in the three Transplant Areas numbered 783, 80, and 339, respectively. Martz figured that seedling production in the three areas totalled 3.6 seedlings per Transplant Area 1, 3.3 seedlings per Transplant Area 2, and 5.7 seedlings per Transplant Area 3. However he also suggested that native *Eriastrum* plants already existing in Areas 2 and 3 may have contributed to these totals.

Date Project Initiated: January 1988.

IV.A.10. *Eriophyllum mohavense* (Barstow Woolly Sunflower): Not State listed; Federal Candidate C2; CNPS List 1B.

Respondent: Mr. James Brownell, California Energy Commission, Sacramento.

Project Name and Description: "Luz SEGS VII." The project involved the construction in 1988 of a solar power plant by the California Energy Commission, at Kramer Junction in San Bernardino County (Mojave Desert). Luz Engineering, the company that was contracted to construct the power plant, attempted to salvage the plant by collecting seed, topsoil, and additional subsoil material, and by depositing these on the receptor site.

The original occurrence of more than 1700 individuals of *Eriophyllum mohavense* on less than 2 acres represented the western-most location of the species, which is one of the main reasons for attempts to preserve this site. The site is also unusual because population densities are much higher here than in other regions where *Eriophyllum mohavense* is found. Also, a soil investigation was conducted by ERT (1988a; Fort Collins, Colorado) to determine whether the distribution of *Eriophyllum mohavense* (and the Mojave spineflower [*Chorizanthe spinosa*]) is controlled by edaphic factors. The report established that there are distinct differences between the soils on the low knolls that support *Eriophyllum mohavense* and adjacent areas that do not. The rare plants apparently grow on areas with a near surface layer (Btn natric horizon) and an underlying "pan" layer (the lower portion of the natric horizon, the Btkn horizon) that are both highly alkaline.

These layers apparently restrict rooting and establishment by spiny saltbush and other common shrubs of the area, but are not restrictive to *Eriophyllum mohavense* that roots above the pan (ERT 1988a). ERT also found very high levels of boron in the soil. This information was used in selection of the receptor site of *Eriophyllum mohavense*.

Mitigation-Related?: Yes.

Project Objectives: The state objective was to re-establish a population of *Eriophyllum mohavense* on a nearby artificially constructed hill. The original location of *Eriophyllum mohavense* was destroyed by the construction of the solar power plant.

Project Methods: According to the biological resources mitigation implementation plan (ERT 1988b), the consulting botanist worked with Mr. Mark Bagley of Bishop, California, to collect surface material (seed, litter, and the top 0.5 inch of topsoil) within a delineated area at the impacted site. This was done to be done with flat-bottomed shovels and other hand tools. The collected material was to be stored temporarily by spreading it on plastic sheets near the relocation site. About 25 percent of the seed source material was to be used to provide supplemental seed to areas of known habitat for *Eriophyllum mohavense*.

Soil was salvaged in three steps after seed collection. The base material was to be applied to the existing surface at the relocation site to increase the southerly aspect of the site to an approximately 4 percent slope. Following application of the base material, more soil was to be placed on the relocation site, spread, and contoured. In the last stage, the seed source was to be applied and raked smooth. The site was to be misted with water to moisten the seed material and help bind it to aid in erosion control. Finally, the relocation site was fenced by the Luz Engineering Corporation to prohibit future disturbance (ERT 1988b).

Criteria for Success: No specific success criteria were established. Respondent reported that the general criteria was to find the species on the relocation site.

Project Success: Respondents claims that at the present time, due to the unusually dry years since this project has occurred, no systematic monitoring has been conducted and no plants have been found. However, they claim that the success is "uncertain" until the desert receives normal rainfall.

Date Project Initiated: 1988.

IV.A.11. *Eryngium aristulatum* var. *parishii* (San Diego Button Celery): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: Drs. C.H. Black and Paul Zedler, Dept. Biology, San Diego State University.

Project Name and Description: "Caltrans Del Mar Mesa Vernal Pools" and "U.S. Navy North Miramar Project Mitigation." As background, California Department of Transportation (Caltrans) had two major projects on Kearny Mesa that eliminated vernal pools. The first project was mitigated by the purchase of 26 acres of prime vernal pool habitat on Del Mar Mesa and a second acquisition of an additional 52 acres at Del Mar Mesa. This second acquisition was to be used in an experiment to create artificial pools capable of supporting *Eryngium aristulatum* var. *parishii* and *Pogogyne abramsii* (Zedler and Black 1988). Respondents did not explain the Mirimar Project. (see IV.A.29 for additional information).

Mitigation-Related?: Yes.

Project Objectives: For both projects, the objective was to create vernal pool habitat for *Eryngium aristulatum* var. *parishii* and *Pogogyne abramsii.*

Project Methods: A set of 40 artificial basins was excavated in December 1986, and 387 were inoculated with material collected from the natural pools on Del Mar Mesa.

Criteria for Success: Respondents did not specifically designate criteria for success.

Project Success: Respondents feel that the projects are "not yet" successful because the rare species have not attained population densities found in the natural pools.

Date Project Initiated: December 1986.

IV.A.12. *Erysimum capitatum* var. *angustatum* (Contra Costa Wallflower): State endangered; Federally endangered; CNPS List 1B.

Respondent: Ms. Joy Albertson, U.S. Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex.

Project Name and Description: "Vaca Dixon-Contra Costa 230-kV Reconductoring Project: Habitat Protection and Enhancement for Antioch Dunes." Pacific Gas and Electric Company (PG&E) reconductored the San Joaquin River crossing of the Vaca Dixon-Contra Costa 230 kV transmission line in the fall of 1988. The project took place specifically on the Sardis Unit of the Antioch Dunes National Wildlife Refuge (ADNWR), east of the town of Antioch. USFWS personnel conducted a Section 7 consultation with PG&E before granting access permit. (see IV.A.25 for more details.)

Mitigation Related?: Yes.

Project Objectives: Objectives were: (1) protection of habitat from future damage caused by construction/repair activities; (2) transplantation of sensitive species from the access corridor to allow vehicle access to the tower; (3) establishment of new subpopulations of *Erysimum capitatum* var. *angustatum* (and *Oenothera deltoides* ssp. *howellii*); (4) enhancement of existing populations; and, (5) determination of whether direct seeding or transplantation of nursery liners is preferable transplantation technique.

Project Methods: Eighteen wallflowers from the PG&E east parcel access corridor were transplanted either to other locations on the parcel or to the Sardis Pit area. A small circular area was first cleared of all vegetation, then an appropriate sized hole was dug. A plant was placed in the hole and dirt was packed firmly around it. Nursery grown plants were planted in a similar manner in pre-selected sites on the PG&E and Sardis Pit parcels.

Three hundred seventy-seven (377) wallflower seedlings were planted in January

1990. A survey the following March provided a count of 364 surviving seedlings (96.6%) survival. Plants were monitored during the first spring and summer to determine whether additional water or weeding was needed so as to assure adequate survival. A final evaluation of survival will be made in the spring of the second year.

Cost of the nursery-grown seedlings was estimated at $0.30/seedling; 377 seedlings produced; therefore it cost $113.10.

Criteria for Success: The replacement of the plants that were destroyed by the construction, specifically 230 *E. capitatum* var. *angustatum* seedlings and 160 *O. deltoides* ssp. *howellii* seedlings was the criterion.

Project Success: Respondent felt that the project was partially successful. Transplantation of the wall flowers resulted in aa final 61.1% survival rate for 18 of the 22 plants, and 0.0% survival of the additional four (4) individuals. However, germination was high and survival of outplanted seedlings was 96.6% in the first year.

Date Project Initiated: April 5, 1989, for transplantation of *E. capitatum* var. *angustatum* individuals; January 1990 for seedling outplanting.

IV.A.13. *Erysimum menziesii* (Menzies' Wallflower): State endangered; Federal Candidate C1; CNPS List 1B.

1) Respondent: Ms. Frederica Bowcutt, State of California Department of Parks & Recreation, Sacramento.

Project Name and Description: None. Project involved the reintroduction of *Erysimum menziesii* and *Chorizanthe howellii* to archeological sites at MacKerricher State Park (Mendocino County) after an archeological dig. University of California, Davis, initiated an archeological dig in 1989-90 at sites containing rare species. (see IV.A.6 for more details.)

Mitigation-Related?: Yes.

Project Objectives: None stated.

Project Methods: Seed was collected in the summer of 1989 from the plants on site before the archeological dig was initiated. Plug plants were grown at the California Conservation Corps (CCC) Napa nursery and outplanted in February 1990 by the CCC. Plants were monitored by an undescribed photo monitoring technique. Outplanted plants also were counted and mapped. Initial costs for the project were: (1) salary $800.00; (2) travel $400.00; and, (3) plants $200.00, for a total of $1400.00.

Criteria for Success: None stated.

Project Success: Project on-going. Information not yet available.

Date Project Initiated: July 1989.

2) Respondent: Ms. Frederica Bowcutt, State of California Department of Parks & Recreation, Sacramento, and data obtained from EPP files.

Project Name and Description: "Spanish Bay." Project involved the reintroduction of *Erysimum menziesii*, *Lupinus tidestromii* var. *tidestromii*, and *Gilia tenuiflora* ssp. *arenaria* to the dunes surrounding the Links at Spanish Bay (Monterey County). (see IV.A.15 and IV.A.22 for more details.)

Mitigation-Related?: Yes.

Project Objectives: To increase the numbers of the three rare plant species and either enhance existing populations or create new stands.

Project Methods: Seed was collected from a population at Asilomar and propagated at Spanish Bay Nursery. Outplanting of seedlings was to occur during the winter rainy season. The populations were to be fenced and signed, and a boardwalk constructed to route foot traffic past the outplantings. Regular maintenance is to include weeding of invasive species.

Criteria for Success: Survivorship of 80% for the total outplanted seedlings in the first year, and a total of 70% of the plants within each distinct outplanting site. Should survivorship fall below these standards, replanting would be required to occur during the next rainy season.

Project Success: Respondent reports that the project appears successful, although no information held in the EPP files confirmed this.

Date Project Initiated: 1987.

3) Respondent: Dr. John Sawyer, Department of Biology, Humbolt State University, Arcata.

Project Name and Description: None. Project involved a three-year research project to study the biology of *Erysimum menziesii* and mitigation techniques. The research was supported by a timber company to mitigate the impacts of their harvest operation.

Mitigation-Related?: Yes.

Project Objectives: Stated objectives were to determined a viable population size and ways of habitat restoration to achieve a viable population size.

Project Methods: The current research project has not included any transplantation, relocation or reintroduction at this date. However, 30 permanent plots in existing populations are monitored quarterly, and have been so for the last two and one-half years. Project costs were given at $650,000.00.

Criteria for Success: Criterion was stated somewhat vaguely as when the existing population exceeds in size that projected by computer modeling.

Project Success: Project was still in progress at the time of the questionnaire.

Date Project Initiated: 1988 is the date given for the beginning of the project, although seed collection commenced in April of 1989.

IV.A.14. *Erysimum teretifolium* (Santa Cruz Wallflower): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: "Revegetation of the Olympia Quarry." The revegetation is to be done in compliance with conditions stipulated in a mining permit administered by Santa Cruz County. The Olympia Quarry is operated by Lone Star Industries, Inc., and is located west of Scotts Valley. The quarry site is approximately 200 acres, the majority of which has been mined for coarse sand for construction.

The adjacent vegetation is considered biologically significant because it is a xeric environment of sand hills in the midst of more mesic vegetation. Some of the rare elements on the quarry site include rare disjuncts or unusual flower color morphs.

Mitigation-Related?: Yes.

Project Objectives: The goal of the revegetation is to establish the Santa Cruz wallflower on the mined slopes and benches of the Olympia Quarry. In addition, a revegetation plan will attempt to recreate the native plant associations on the previously mined areas.

Project Methods: Larry Seeman and Associates, Inc. (LSA 1989) proposes to collected 50% of all the seed produced by a group of 300 plants growing in the eastern section of the quarry. The planting areas are composed of 15-ft wide benches at 60-ft intervals along a 1.5:1 slope. The seeding regime is to replicate the density of the *Erysimum teretifolium* in undisturbed communities.

Criteria for Success: Criteria will be developed by quantitatively sampling the vegetation in areas with *Erysimum teretifolium*.

Project Success: Project is not yet implemented. Information not yet available.

Date Project Initiated: Revegetation Plan initially submitted by LSA Associates, Inc. in July 1987 (LSA 1987, 1989). The project has not yet begun, however.

IV.A.15. *Gilia tenuiflora* ssp. *arenaria* (Sand Gilia): State threatened; Federal Candidate C1; CNPS List 1B.

Respondent: Ms. Frederica Bowcutt, State of California Department of Parks & Recreation, Sacramento, and data obtained from EPP files.

Project Name and Description: "Spanish Bay." Project involved the reintroduction of *Erysimum menziesii*, *Lupinus tidestromii* var. *tidestromii*, and *Gilia tenuiflora* ssp. *arenaria* to the dunes surrounding the Links at Spanish Bay (Monterey County). (see IV.A.12(2) and IV.A.22 for more details.)

Mitigation-Related?: Yes.

Project Objectives: To increase the numbers of the three rare plant species and either enhance existing populations or create new stands.

Project Methods: Seed was collected from a population at Asilomar and propagated at Spanish Bay Nursery. Seeds of sand gilia need stratification and scarification with differing daylength and temperature regimes. Outplanting of seedlings was scheduled to occur during the winter rainy season. The populations were to be fenced and signed, and a boardwalk constructed to route foot traffic past the outplantings. Regular maintenance was to include weeding of invasive species.

Criteria for Success: Survivorship of 80% for the total outplanted seedlings in the first year, and a total of 70% of the plants within each distinct outplanting site. Survivorship was to be compared in outplanting sites with existing populations in an attempt to account for annual fluctuations that may be environmentally controlled. Should survivorship fall below these standards, replanting would be required to occur during the next rainy season.

Project Success: Respondent reports that the project appears successful, although no information in the EPP files confirmed this.

Date Project Initiated: 1987.

IV.A.16. *Hemizonia increscens* ssp. *villosa* (Gaviota Tarplant): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: Mr. John Storrer, Storrer & Semonsen Environmental Services, Santa Barbara.

Project Name and Description: "Gaviota Interim Marine Terminal, Santa Barbara County, California." Mitigation was required for the construction of a secondary access road to the marine terminal.

Mitigation-Related?: Yes.

Project Objectives: The stated objective was the establishment of 5,800 ft^2 of *Hemizonia increscens villosa* habitat.

Project Methods: The impacted site was surveyed for *Hemizonia increscens* ssp. *villosa* and it was determined that approximately 50 individuals lay within the access road alignment. There are considerably more individuals found adjacent to the area (approximately 400-600 individuals). Seed was obtained from plants collected from the tank farm area prior to construction. An additional 2-3 inches of topsoil was retrieved before grading. More topsoil (3 inches) also was removed from the access road alignment during grading. The receptor site is on California Department of Parks and Recreation property east of the Texaco Interim Marine Terminal. No further site preparation was attempted prior to broadcasting of seed. The receptor site was fenced with three strands of barbless wire to delineate boundaries, and the project was signed.

Additional (approximately) 50 tarplant seedlings were discovered during an inspection of the site in March 1989. Adjacent weedy vegetation was clipped within a 6 inch radius of many of the plants to decrease competition.

Criteria for Success: Performance criteria included: (1) no evidence of soil erosion; and, (2) presence of a viable *H. increscens* ssp. *villosa* population. The latter was determined by comparing the density of flowering plants during the peak growing period with that of the surrounding populations.

Project Success: An intensive survey was conducted on May 24, 1989, that recorded 136 flowering tarplants, with an additional nine plants that had died or seeded. The first year densitites of 1.2, 2.69 and 1.28 individuals per m^2 recorded were favorable in comparison with the Chevron restoration site. The project is on-going; however, the respondent felt that the first year's results were promising. More information is not yet available.

IV.A.17. *Hemizonia minthornii* (Santa Susana Tarplant): State rare; Federal Candidate C2; CNPS List 1B.

1) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Santa Susana Tarplant (*Hemizonia minthornii*) Mitigation Program 2." Las Virgenes Municipal Water District built a new water reservoir adjacent to its existing reservoir in the Twin Lakes area near Chatsworth. Mitigation for this project involved the salvaging of *Hemizonia minthornii* plants, and transplanting the salvaged plants and some nursery plants grown from seed on the 250 m^2 cut slopes surrounding the new reservoir.

Mitigation-Related?: Yes.

Project Objectives: The overall project objective was to establish a new population of Santa Susana tarplants on the cut slopes surrounding the new water reservoir.

Project Methods: The project site boundaries were staked prior to the initiation of the construction. Seeds were collected in the summer of 1988 at a time considered by the consultants as not phenologically optimum for success -- *i.e.*, while the plants were in full bloom. Individual plants were located in either rock crevices or on thin soil in open areas. A pick mattock was used to break up the sandstone crevices to remove the top portion of the root, but the root was very deeply embedded in the substrate and could not be removed without breaking.

Potting mix was brought to the site and mixed with clean sand and soil from the site. Each transplanted plant was trimmed with clippers to compensate for the loss of the root system, and then potted. Each transplant was watered several times before transportation to Tree of Life Nursery. Cuttings were taken from the transplants and retained for their inflorescences and to attempt root cuttings. A total of 55 plants were potted, representing approximately 70% of the mature plants within the impacted area. Approximately 50% survived the initial transplantation operation; however, cutting survival and seed germination were poor (McClelland Consultants (West), Inc. 1988). None of the initial seed sown germinated (McClelland Consultants (West), Inc. 1988). A second collection of seed made in October 1988 was germinated at Tree of Life Nursery to compensate for the losses.

As of February 1989, however, only 8 of the 55 transplants have survived. During 1990, the site was visited and monitored only 4 times, as the plants appeared to show signs of naturalizing to the cut slope.

Criteria for Success: Performance criteria included the following: (1) 15 surviving mature plants from the transplants by May 1989; (2) 50 seedlings by May 1989; (3) 10 mature plants flowering by October 1989; (4) 30 mature plants by October 1990; (5) 100 seedlings by October 1990; (6) 50 mature plants by October 1991; (7) 70 mature plants with ground coverage of about 25 m^2 by October 1992 (McClelland Consultants (West) 1988).

Project Success: The project success has not been evaluated only because the project technically is still on-going. However, the survival of 8 of the 55 transplants, only 7 of which are doing well, is rather poor (McClelland Consultants (West) 19908). The project has been rather controversial (see article in the Los Angeles Times, February 3, 1989, p. 3, 14).

Date Project Initiated: July 1988 for the initial collection of seed and excavation of plants in the impacted area; January 1989 for the transplantation of salvaged plants.

2) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Woolsey Canyon Development." Chateau Builders proposed in 1989 to construct an extensive residential community in Woolsey Canyon, western Los Angeles County. The project site is located in a sensitive ecological areas as designated by Los Angeles County. An environmental assessment performed by Michael Brandman & Associates (November 1988) identified that the proposed project would result in the direct loss of approximately 57 individuals of *Hemizonia minthornii*, in a population of approximately 147 individuals.

Mitigation-Related?: Yes.

Project Objectives: The primary objective of the mitigation plan will be: (1) to establish on the development site, a second population of *Hemizonia minthornii*, using propagules derived from individuals in the original population that is impacted by the development. The new population should be capable of natural regeneration over the long term; (2) offset of the loss of approximately 57 individuals of *Hemizonii minthornii* with the introduction of approximately 150 individuals as a founder group in a new population; and, (3) advance the state of knowledge of *Hemizonii minthornii* by carrying out appropriate research-related activities in conjunction with mitigation activities (Mistretta 1989).

Project Methods: The plants occur within a single population on a sandstone outcrop on the project site. The original development plan was designed to include 90 individuals in a reserve that would be bordered by the development. However, after consultation with CDFG, the reserve site was reconfigured to be continuous with an adjacent natural area on the southern boundary of the project, rather than being an island within the development (Mistretta 1989).

The Rancho Santa Ana Botanic Garden (RSABG) has been retained by the Chateau Group to advise on the horticultural and research-related aspects of the program. Data to be gathered are: (1) number of individuals on site; (2) soil analyses; (3) population statistics; (4) reproductive capacity; (5) genetic composition; and, (6) floristic composition of the community.

The proposed revegetation program indicates that prior to the commencement of construction, the preserve site will be fenced and left undisturbed. The remaining Santa Susana tarplants will have the infructescences removed by hand at the appropriate season. Additional seed collection will be done if deemed necessary. Collected seed will be cleaned and dried prior to storage.

Half the collected seed will be sown in the preserve after the transplantation of salvaged individuals (see below). The remaining half will be propagated at RSABG for seedling transplantation.

In addition, the mature plants in the impacted area will be salvaged by digging with a shovel and pick mattock to a depth of 1 ft. Plants will be placed in planters for temporary off-site storage. Plants will be trimmed and watered 3 times during the first week and weekly thereafter until transplanted.

Transplant receptor sites within the preserve will be selected by a botanist/horticulturalist. Plants will be planted without mulch or fertilizers, and watered weekly for 4 weeks. The project site will be checked monthly by the botanist/horticulturalist for an undetermined period.

IV.A.18. *Holocarpha macradenia* (Santa Cruz Tarplant): State endangered; Federal Candidate C1; CNPS List 1B.

1) Respondent: None. Data obtained from EPP files.

Project Name and Description: "Hilltop Commons Development." The Nylen Company, Inc., developed an apartment complex in Pinole, Contra Costa County. Dr. Neil Havlik, then of the East Bay Regional Park District, agreed to perform a salvage of the mature individuals of *Holocarpha macradenia* from the project site and transplant them to a nearby park within the East Bay Regional Park District.

Mitigation-Related?: Yes.

Project Objectives: None specifically stated, but the project was designed to salvage the mature plants of *Holocarpha macradenia* from a housing development site in Pinole, and subsequently establish a new population of *H. macradenia* at Wildcat Canyon Regional Park.

Project Methods: Pallets of soil, 4 ft^2 by 1 ft deep, containing *Holocarpha macradenia* plants were dug and seed was collected from these plants. Seed from the salvage was taken by Dr. Havlik and spread as an enlargement of several existing populations in Wildcat Canyon Park (Havlik's Stand Nos. 2, 11, 12, 13, 14, 15; [CNDDB Occ. Nos. 2, 29, 31 for the first three locations]). Seed also was spread at a site in Sather Canyon on the east side of San Pablo Reservoir.

Criteria for Success: None stated.

Project Success: Havlik monitored 21 populations, 7 of which were new populations, and reported an increase of 30% of the individuals from 1985 to 1986[10].

Date Project Initiated: September 13, 1986.

IV.A.19. *Lasthenia burkei* (Burke's Goldfields): State endangered; Federal Candidate C2; CNPS List 1B[11].

1) Respondent: Mr. Charlie Patterson, Plant Ecologist, private consultant, El Cerrito, and

[10]See letter to Ms. Susan Cochrane, [formerly] Endangered Plant Coordinator, from Dr. N. Havlik, [formerly of the] East Bay Regional Park District, dated March 9, 1987.

[11]Mr. Ken Milam, Sonoma County Planning Director, returned a questionnaire for *Lasthenia burkei*, but the information provided was so vague as to be useless for this analysis. Therefore, the questionnaire is not included.

data obtained from EPP files.

Project Name and Description: " Airport Boulevard Business Park." A business park was constructed in 1984, located just northeast of the Sonoma County Airport.

Mitigation-Related?: Yes.

Project Objectives: The stated objective for the mitigation for the business park was the replacement of 0.3 acres of wetlands and pre-existing 5000 individuals of *Lasthenia burkei* with, at minimum, 10,000 individuals.

Project Methods: Seed was collected in 1984. Small pools were created by hand, clearing vegetation and topsoil in low swales within an 100 ft easement. These pools were seeded during the winter of 1985-1986. However, much of the easement was disturbed by the installation of a large storm drain before the seeding trials could be assessed. However, new larger pools were created later by a bulldozer-mounted blade during the fall of 1986, and seeded that year.

Criteria for Success: Essentially the replacement of a self-sustaining colony of *Lasthenia burkei* was the criterion for success.

Project Success: Respondent felt that the project was successful. The mitigated seeded population increased from no *Lasthenia burkei* to >6000 individuals in three years. However, due to additional complications, the pools were "re-worked" (*i.e.*, enlarged, re-contoured and re-seeded). The current year's results show in excess of 10,000 individuals.

2) Respondent: Mr. Charlie Patterson, Plant Ecologist, private consultant, El Cerrito, and data obtained from EPP files.

Project Name and Description: "Sonoma County Airport". This project involved the contruction of a new, paved apron at the Sonoma County Airport in 1986.

Mitigation-Related?: Yes.

Project Objectives: Objectives stated by the respondent for the airport expansion project was the replacement of the colony of *Lasthenia burkei* lost during construction.

Project Methods: Eleven small artificial pools were created by shovel and hoe in a broad, nearly level portion of the infield between the north end of Runway 14 and Taxiway Y. Pools were made by selecting a low spot and then scraping 1 to 6 inches of the surface. The scraped soil was piled into small berms around the downslope edges of the pools. Pools were seeded the day of construction.

Seed was sown both as seed collected in 1985 and from other existing populations 0.5 miles away, and by spreading the scraped topsoil from nearby colonies. These were then left alone for most of the winter and spring. Pools were monitored, which involved checking them for water collection and holding capacity, *Lasthenia burkei* germination, phenology, and reproduction.

Criteria for Success: Essentially the replacement of a self-sustaining colony of *Lasthenia burkei* was the criterion for success.

Project Success: Respondent felt that the project was successful. Seeded areas of existing ditches now support several thousand individuals of *Lasthenia burkei*, and another several thousand are growing in the constructed pools.

3) Respondent: Carl Wilcox, California Department of Fish and Game, Yountville, and data obtained from EPP files.None. Data obtained from EPP files.

Project Name and Description: "Santa Rosa Rare Plants Mitigation Plan San Miguel Estates 1." In 1989 Cobblestone Development Corporation proposed the development of San Miguel Rancho Subdivision (RSM) at 2001 Waltzer Road within the city of Santa Rosa, Sonoma County and San Miguel Estates No. 2 (SME) at 2192 Francisco Avenue, also within Santa Rosa. The SME project is an on-going housing construction and the RSM housing project was a 1989 development. The projects would destroy approximately

2.51 acres of vernal pool habitat. (see IV.A.2(2) for more details.)

Mitigation-Related?: Yes.

Project Objectives: According to the Mitigation Agreement between Cobblestone and CDFG, the mitigation should establish self-sustaining populations of plants in approximately 2.97 acres of newly created habitat on the mitigation site. Self-sustaining is defined as approximately 13,000 individuals of *Lasthenia burkei* and 137,000 individuals of *Blennosperma bakeri* for 2 consecutive years without supplemental seeding.

Project Methods: The mitigation plan was devised by R. Osterling, Inc. (1989). The plan proposed to transplant all existing plants and/or seeds to a 20-acre receptor site located approximately 1.5 miles west of the San Miguel Estates property, with existing 3.49 acres of vernal pool resources. Approximately 2.5 acres of vernal pool habitat will be constructed at the receptor site with pool configuration and depth based on survey of existing pools. Grading will be done with small equipment under supervision of a qualified botanist (Charlie Patterson, private consultant). Plant material will be "transferred." Seed will be collected from donor pools and the top 1-2 inches of pool bottom duff will be excavated and spread in the excavated pools at the receptor site. Monitoring will continue through June 1991.

Criteria for Success: None explicitly stated.

Project Success: Respondent indicated that although it was too early to tell because the projects are only in their first year, "[e]arly indications are that they will be the most successful relocations yet achieved in the Santa Rosa Area."

Date Project Initiated: March 1989.

4) Respondent: WESCO, Novato.

Project Name and Description: "County of Sonoma Public Service Area 31 Waste Water Storage Pond." The project involved the creation of a wastewater storage pond in 1988 on approximately 3.7 acres of northern vernal pool, seasonal marsh and intermittent stream habitat (and 10 acres of non-native grassland). *Lasthenia burkei* was transplanted to an area known as "The Wildflower Preserve" on the Sonoma County Airport. The receptor site is already protected as part of the Sonoma County Airport mitigation.

Mitigation-Related?: Yes.

Project Objectives: The project objective was to create 4.4 acres of seasonal wetland habitat and to provide a transplantation site for *Lasthenia burkei.*

Project Methods: Seed was collected from plants at the impacted site. Plants in bloom were salvaged, kept in containers until seeded and seed subsequently was collected to be sown at the mitigation site. Topsoil was salvaged from around the plants to spread at the new sites.

The number of individuals are to be counted for each of five years.

Criteria for Success: Criteria have not been established.

Project Success: "Although the criteria have not been established, we feel that, for at least the first year of monitoring, the transplantation was somewhat successful. . . . Of course, long term viability of the population is still questionable." Approximately 1000 individuals were observed at the mitigation site, while only 150 plants were found at the impacted site.

Date Project Initiated: 1988.

IV.A.20. *Lilaeopsis masonii* (Mason's Lilaeopsis): State rare; Federal Candidate C2; CNPS List 1B.

1) Respondent: Mr. Niall McCarten, Department of Integrative Biology, University of California, Berkeley, and Department of Water Resources (DWR), Sacramento (questionnaire unsigned).

Project Name and Description: "California Department of Water Resources (DWR) Barker Slough Bank Revetment." The project was initiated in 1989 by DWR for levee bank protection on private property. Individuals of *Lilaeopsis masonii* were transplanted from the east side of the slough to the west side.

Mitigation-Related?: Yes.

Project Objectives: Project objectives were the removal of *Lilaeopsis masonii* from the proposed rip-rap site and the transplantation of individuals to suitable habitat.

Project Methods: Populations of *Lilaeopsis masonii* were removed with a shovel, placed in shallow water in plastic containers and then placed in a boat and transported to the potential habitat (receptor site). After placing the transplant into the new site, the surrounding substrate was pressed along the edges to homogenize the substrate.

Eighteen (18) 50 x 50 cm permanent plots were established, and marked with numbered, color-coded metal stakes (ECOS, Inc. 1988). Control populations were marked similarly. All plants were to be counted in each plot five times during the first two years following transplantation, and three times per year for the following three years.

The receptor site initially was not protected, but due to the biological values of the site, it was purchased by CDFG as a preserve in January 1990.

Criteria for Success: Specific criterion was the survival of 80% or better of the individuals transplanted over a 5-year monitoring period.

Project Success: Unknown, as the project is on-going. One year of raw data is available from Mr. David Brown, DWR. DWR respondent claims that it is too early to make a determination as to whether the project is successful.

Date Project Initiated: April 1989

2) Respondent: Ms. Frederica Bowcutt, State of California Department of Parks & Recreation, Sacramento.

Project Name and Description: None. Project is being considered; may involve the transplantation of *Lilaeopsis masonii* at Brannan Island State Recreational Area near Rio

Vista (Contra Costa County).

Mitigation-Related?: Yes.

Project Objectives: Project still being planned. None stated.

Project Methods: Project still being planned. None stated.

Criteria for Success: Project still being planned. None Stated.

Project Success: Project still being planned. Not applicable.

Date Project Initiated: Not yet initiated.

IV.A.21. *Lupinus milo-bakeri* (Milo Baker's Lupine): State threatened; Federal Candidate C2; CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: None. In 1985, California Department of Transportation (Caltrans) performed road maintenance along State Highway 162 (Mendocino Pass Road) near the city of Covelo (Mendocino County). The mitigation project was to offset the impacts of this activity.

Mitigation-Related?: Yes.

Project Objectives: None stated explicitly, but the project was to establish several new populations to offset the loss of *L. milo-bakeri* during highway maintenance.

Project Methods: Caltrans collected seed from the CNDDB occurrence #2 for *Lupinus milo-bakeri* from August through September 1985. Not more than 15% of the population's annual seed crop was collected. Prior to seeding, the collected seed was rinsed, and the seed beds prepared by adding topsoil from the parent population. In October 1985, Caltrans planted the seed in areas of suitable habitat along Highway 162 between post mile markers (PM) 31.50 and 31.61, and from PM 32.00 to 32.14, as well as planted seed in suitable habitat near the Caltrans equipment yard near Covelo.

Criteria for Success: None stated.

Project Success: In some of the plots, there was considerable competition from annual grasses. Caltrans annually sprays the highway edges with herbicide, and this added to the growth of *L. milo-bakeri* in the seeded areas.

Date Project Initiated: August 1985.

IV.A.22. *Lupinus tidestromii* var. *tidestromii* (Tidestrom's Lupine): State endangered; Federal Candidate 1; CNPS List 1B.

Respondent: Ms. Frederica Bowcutt, State of California Department of Parks & Recreation, Sacramento, and data obtained from EPP files.

Project Name and Description: "Spanish Bay." Project involved the reintroduction of *Lupinus tidestromii* var. *tidestronii*, *Erysimum menziesii*, and *Gilia tenuiflora* ssp. *arenaria* to the dunes surrounding the Links at Spanish Bay (Monterey County). (see IV.A.13(2) and IV.A.15 for additional details)

Mitigation-Related?: Yes.

Project Objectives: To increase the numbers of the three rare plant species and either enhance existing populations or create new stands.

Project Methods: Seed was collected from a population at Asilomar and propagated at Spanish Bay Nursery. Seeds of *Lupinus tidestromii* var. *tidestromii* need stratification and scarification with differing daylength and temperature regimes. Outplanting of seedlings was to occur during the winter rainy season. The populations were to be fenced and signed, and a boardwalk constructed to route foot traffic past the outplantings. Regular maintenance was to include weeding of invasive species. Monitoring will continue until 1993.

Criteria for Success: Survivorship of 80% for the total outplanted seedlings in the first year, and a total of 70% of the plants within each distinct outplanting site. Should survivorship fall below these standards, replanting would be required to occur during the next rainy season.

Project Success: Respondent reports that the project appears successful, although no information in the EPP files confirmed this.

Date Project Initiated: 1987.

IV.A.23. *Mahonia nevinii* (Nevin's Barberry): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: None. The RANPAC Corporation proposed the construction of Vesting Tentative Tract No. 23267 that would impact a population of *Mahonia nevinii* on the Old Vail Ranch property. Although 12 plants are found on the property, the mitigation project involved the relocation of a single plant.

Mitigation-Related?: Yes.

Project Objectives: None stated explicitly.

Project Methods: The impacted plant would undergo crown division and root cuttings. These would be transplanted in the late fall (no more details were provided). The success of the transplantations would be monitored for three years following transplantation. Seed was to be collected in the summer of 1989 to be propagated in a nursery and maintained until the success of the transplantation efforts could be adequately assessed.

Criteria for Success: Success would be based on the number of (trans)plants that grow and reproduce.

Project Success: Unknown. No information available in EPP files.

Date Project Initiated: Fall 1988.

IV.A.23. *Monardella linoides* ssp. *viminea* (Willowy Monardella): State endangered; Federal Candidate C3; CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: None. Mitigation was required for the California Department of Transportation (Caltrans) construction in 1983 of an I-15 gap closure and the construction of State Route 52 from I-805 to Santo Road.

Mitigation-Related?: Yes.

Project Objectives: The project objective was simply to offset losses of this plant species caused by construction of the highway projects.

Project Methods: For the State Route 52 project, Caltrans collected a total of 55 individual *M. linoides* ssp. *viminea* plants within the impacted area, and collected green cuttings of this species for reintroduction into suitable habitat within the project area. For the two projects together, Caltrans collected no more than 50% of each year's seed from populations within the impacted area. Prior to broadcasting of seed, Caltrans reviewed existing sites to characterize the ecological parameters of the species.

Criteria for Success: None stated explicitly.

Project Success: Progress reports were submitted in November 1983, April 1984, June 1985, and May 1986. The 1986 report stated that from June 1985 to December 1985, approximately 389 (additional) seedlings died, from the earlier total of 509 plants. This was the result of overcrowding in the nursery.

Two of the original 16 containerized salvaged plants died by June 1985. By December 1985, an additional eight plants had died.

Findings in the 1986 report were: (1) salvaged *M. linoides* ssp. *viminea* plants required parent soil to survive; (2) plants in nursery conditions need to be aggressively pruned; (3) nursery containers must be widely spaced; (4) *M. linoides* ssp. *viminea* is easily propagated from seed and cuttings, and, (5) transplantation would be at a suitable site in Murphy Canyon.

Date Project Initiated: 1983.

IV.A.25. ***Oenothera deltoides* ssp. *howellii*** (Antioch Dunes Evening Primrose): State endangered; Federally endangered; CNPS List 1B.

Respondent: Ms. Joy Albertson, U.S. Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex.

Project Name and Description: "Vaca Dixon-Contra Costa 230-kV Reconductoring Project: Habitat Protection and Enhancement for Antioch Dunes." Pacific Gas and Electric Company (PG&E) reconductored the San Joaquin River crossing of the Vaca Dixon-Contra Costa 230 kV transmission line in the fall of 1988. The project took place specifically on the Sardis Unit of the Antioch Dunes National Wildlife Refuge (ADNWR), east of the town of Antioch. USFWS personnel conducted a Section 7 consultation with PG&E before granting access permit. (see IV.A.12 for more details.)

Mitigation Related?: Yes.

Project Objectives: Objectives were: (1) protection of habitat from future damage caused by construction/repair activities; (2) transplantation of listed species from access corridor to allow vehicle access to the tower; (3) establishment of new subpopulations of *Oenothera deltoides* ssp.*howelii* (and *Erysimum capitatum* var. *angustatum*); (4) enhancement of existing populations; and, (5) determination of whether direct seeding or transplantation of nursery liners is preferable.

Project Methods: Plants from the PG&E east parcel access corridor were transplanted either to other locations on the parcel or to the Sardis Pit area. A small circular area was first cleared of all vegetation, then an appropriately sized hole was dug. A plant was placed in the hole and soil was firmly packed around it. Nursery grown plants were planted in a similar manner in pre-selected sites on the PG&E and Sardis Pit Parcels.

Seed germination for *Oenothera deltoides* ssp. *howellii* was poor: only 10 seedlings survived to be planted. More seedlings were to be outplanted in December 1990. Cost of the nursery-grown seedlings was estimated at $0.30/seedling; 377 seedlings produced; therefore it cost $113.10.

Criteria for Success: The replacement of the plants that were destroyed by the construction, specifically 160 *O. deltoides* ssp. *howellii* seedlings and 230 *E. capitatum* var. *angustatum* seedlings was the criterion.

Project Success: Respondent felt that the project was partially successful.

Date Project Initiated: April 5, 1989, for transplantation; January 1990 for seedling outplanting.

IV.A.26. *Opuntia basilaris* ssp. *treleasei* (Bakersfield Cactus): State endangered; Federal endangered; CNPS List 1B.

1) Respondent: James Brownell, California Energy Commission, Sacramento.

Project Name and Description: "Kern River Cogeneration Power Plant Project." Project involved the construction of a cogeneration power plant along the Kern River in 1983-85.

Mitigation-Related?: Yes.

Project Objectives: Objective of the mitigation project was to keep the cactus located at the edge of the road from being destroyed by truck traffic during construction.

Project Methods: Cactus pads were collected and allowed to callus. Approximately two weeks later, the pads were taken to the transplantation site. The receptor site is within the California Living Museum (CALM) property, a non-profit, privately-run educational program. CALM is located east of Bakersfield within the native range of *Opuntia basilaris* var. *treleasei*.

The receptor site had been weeded to remove non-native annual grasses, and soil had been loosened to allow the callus end of the pads to be placed in the soil. One hundred fifteen (115) cactus pads were positioned in nine (9) clumped in two (2) nearby areas. The receptor site was visited each year for three (3) years, and grasses were cleared at each visit.

Criteria for Success: Success was achieved if the cactus flourished at the site.

Project Success: The project was considered successful, because the new plants were established wherever pads were planted.

Date Project Initiated: October 1983.

2) Respondent: Rick York, California Energy Commission, Sacramento, and data obtained from EPP files.

Project Name and Description: "Sycamore Cogeneration Project." Project involved the mitigation of operation activities of the Sycamore Cogeneration Company. A population of *Opuntia basilaris* var. *treleasei* became vulnerable to loss from erosion on a slope that was cut prior to construction of the project.

Mitigation-Related?: Yes.

Project Objectives: Sycamore Cogeneration Company, as part of the conditions of certification by the California Energy Commission, agreed to protect *Opuntia basilaris* var. *treleasei* in the main power plant area, pipeline right-of-ways, transmission line right-of-ways, access roads and the fuel oil storage area. If the Bakersfield cactus was disturbed, Sycamore agreed to transplant the affected stands to another area within the project vicinity in a manner similar to that described for the Kern River Cogeneration Project.

Project Methods: No details are provided in the Mitigation Agreement (MA). Information in EPP files indicates that Sycamore Cogeneration Company objected to the five-year monitoring stipulation in the MA.

Criteria for Success: No information was received.

Project Success: No information was received.

Date Project Initiated: 1989.

IV.A.27. *Orcuttia viscida* (Sacramento Orcutt Grass): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: Mr. Barry Hecht, Balance Hydrologics, Inc., Berkeley.

Project Name and Description: "Sunrise/Douglas Wetland Protection and Creation Program", Sacramento County. Project involved mitigation for two housing developments along Sunrise Boulevard, Sacramento County. Techniques for mitigation relocation/transplantation are "pending."

Mitigation-Related?: Yes.

Project Objectives: The objective for both projects was to re-establish species in vernal pools and freshwater seasonal wetlands within a 350-acre wetland preserve.

Project Methods: Methods are "pending."

Criteria for Success: Respondent reports two specific criteria: 1) Survival for 5 years in 90% of the pools and wetlands to which individuals of *Orcuttia viscida* are transplanted; and, 2) noticeable vigor and expansion of the range of *Orcuttia viscida* in 50% of the pools/wetlands into which individuals are transplanted.

Project Success: Decision of success is "pending."

Date Project Initiated: Project is "on-going;" presumably construction has not yet begun.

IV.A.28. *Pentachaeta lyonii* (Lyon's Pentachaeta): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: Mr. Carl B. Wishner, Envicom Corporation, Calabasas.

Project Name and Description: "Lake Sherwood Golf Course." The mitigation that was prepared by Envicom Corporation involved a salvage and restoration plan for *Pentachaeta lyonii* at the Lake Sherwood Golf Course site in Ventura County. The planning unit (Planning Unit No. 1) consisted of a 163-acre golf course, driving range, clubhouse, 146 single-family lots, and 4 estate lots, ranging from 0.3 to 12.7 acres.

Mitigation-Related?: Yes.

Project Objectives: Project objectives included: (1) maintenance of at least one site occurrence of *Pentachaeta lyonii* in perpetuity; (2) maintenance of at least one occurrence in an undisturbed state until the majority has flowered and seeded; (3) harvest of mature seed to establish a "germ plasm" collection at the Rancho Santa Ana Botanic Garden (RSABG), and to establish a living collection; (4) removal of top soil at impacted site for seed collection; (5) development of a five-year monitoring program; and, (6) conduction of a phytosociological study to determine habitat parameters.

Project Methods: Seed of *Pentachaeta lyonii* was collected by hand and by using a portable hand vacuum, yielding 7.75 grams. It was held cryogenically by the RSABG. Just before site grading, a target soil removal from areas of high plant density (70 flats of soil) was conducted, followed by overall surface scraping and stockpiling of about 2 yd^3 of soil.

Salvaged soil was redistributed of 0.1 acre *ex situ* just prior to the first major fall storm (November 1988). A small amount of seed and three (3) flats of salvaged soil were distributed onto the preserved *P. lyonii* location.

Prior to the extirpation of the *Pentachaeta lyonii* site, a grid system of 1 m squares was established using string and nails. Presence and ranked order estimates of density for each square meter were recorded. The identity of all species present within the areal extent of *P. lyonii* was recorded. A random sample of 60 quadrats was investigated for species presence. These data were subjected to an ordination analysis, along with similar data from other sites of occurrence. The *ex situ* site was similarly gridded in the spring of 1989. All species were recorded, and each quadrat checked for *Pentachaeta lyonii*.

Criteria for Success: Respondent indicated that the plan did not specifically designate criteria for success.

Project Success: Success in the stated context was not achieved. The respondent suggested that the plan for salvage was inadequate.

Date Project Initiated: May 1988.

IV.A.29. *Pogogyne abramsii* (San Diego Mesa Mint): State endangered; Federally endangered; CNPS List 1B.

Respondent: Drs. C.H. Black and Paul Zedler, Dept. Biology, San Diego State University.

Project Name and Description: "Caltrans Del Mar Mesa Vernal Pools" and "U.S. Navy North Miramar Project Mitigation." As background, California Department of Transportation (Caltrans) had two major projects on Kearny Mesa that eliminated vernal pools. The first project was mitigated by the purchase of 26 acres of prime vernal pool habitat on Del Mar Mesa and a second acquisition of an additional 52 acres at Del Mar Mesa. This second acquisition was to be used in an experiment to create artificial pools capable of supporting *Pogogyne abramsii* and *Eryngium aristulatum* var. *parishii* (Zedler and Black 1988). Respondents did not explain the Mirimar Project. (see IV.A.11 for additional information).

Mitigation-Related?: Yes.

Project Objectives: For both projects, the objective was to create vernal pool habitat for *Eryngium aristulatum* var. *parishii* and *Pogogyne abramsii*.

Project Methods: A set of 40 artificial basins was excavated in December 1986, and 387 were inoculated with material collected from the natural pools on Del Mar Mesa.

Criteria for Success: Respondents did not specifically designate criteria for success.

Project Success: Respondents feel that the projects are "not yet" successful because the rare species have not attained population densities found in the natural pools.

Date Project Initiated: December 1986.

IV.A.30. *Pseudobahia peirsonii* (Tulare Pseudobahia): State endangered; Federal Candidate C1; CNPS List 1B.

Respondent: John Stebbins, California State University, Fresno.

Project Name and Description: "Round Mountain Flood Control Project," initiated by the Fresno County Metro Flood District. Project plans are being drafted at this time.

Mitigation-Related?: Yes.

Project Objectives: Project plans are being drafted at this time. Net yet available.

Project Methods: Project plans are being drafted at this time. Net yet available.

Criteria for Success: Project plans are being drafted at this time. Net yet available.

Project Success: Net yet available.

Date Project Initiated: Presumably the project has not yet begun.

IV.A.31. *Sedum albomarginatum* (Feather River Stonecrop): Not State listed; Federal Candidate C1; CNPS List 1B.

Respondent: Sharon Villa, California Department of Transportation (Caltrans), Redding.

Project Name and Description: "Feather River Canyon Storm Damage Repair." The project involved the repair of the February 1986 storm damage to State Route 70 in Plumas County. Work included widening at three (3) spot locations where the highway was reduced to a single lane. Initially, the existing rock slopes were cut back approximately 15 feet to restore two traffic lanes. The roadway was later realigned away from the East Branch North Fork Feather River.

Mitigation-Related?: Yes (for a federal candidate).

Project Objectives: The overall goal of the mitigation project was to reduce the severity of project impacts on *Sedum albomarginatum*. Specific project objectives were : (1) avoid unnecessary or inadvertent damage to the population by restricting habitat disturbance to those areas that are located within the slope lines; (2) salvage individual *S. albomarginatum* plants from project impact areas prior to construction, and reintroduce these plants on suitable slopes within the immediate area following construction; (3) collect information on the distribution, density, and microhabitat preferences of *S. albomarginatum* within the project area to guide reintroduction efforts; and, (4) monitor the survival of re-established plants for a period of five years to evaluate the effectiveness of transplantation as a mitigation measure of *Sedum albomarginatum*.

Project Methods: An unspecified number of plants (up to 500 individuals) were salvaged from the impacted site, placed in a burlap bag and transferred to labeled flats. These were maintained in a lath house at the Butte College horticultural facility. The salvaged plants were returned to the area of origin and transplanted after the new highway slopes had been constructed. Two plantings were performed, one in Fall 1986 and the other in Spring 1987. Each plant was permanently marked with a numbered aluminum tag wired to a steel spike driven into the ground.

Criteria for Success: None were developed.

Project Success: One hundred fifty eight (158) plants were outplanted in Fall 1986 and an additional 158 were outplanted the following spring. Only 14 (8.8% survival rate) survived the fall transplant, and only three (3) individuals (1.9% survival rate) survived the spring transplant.

Date Project Initiated: June 1986.

IV.A.32. *Sidalcea pedata* (Bird-Footed Checkerbloom): State endangered; Federally endangered; CNPS List 1B.

Respondent: None. Data obtained from EPP files.

Project Name and Description: "*Sidalcea pedata* Transplantation Project." The project involved the construction of a store (Big Bear K-Mart) in the city of Big Bear Lake (San Bernadino County). The mitigation involved the transplantation of eleven (11) whole plants.

Mitigation-Related?: Yes.

Project Methods: Terms of the Mitigation Agreement (MA) between CDFG and K-Mart Corporation stipulated that all four *Sidalcea pedata* plants on the impacted site were to be translocated to a protected site approximately 0.25 miles away, owned by The Nature Conservancy. However, by the time the MA was signed, several individuals of *S. pedata* were destroyed by equipment operations from an industrial contractor's yard adjacent to the K-Mart proposed site. The remaining twelve plants (10 mature and two seedlings) were transplanted by means of a Vermeer hydraulic spade during November 1988.

Site preparation included the removal of several tons of asphalt debris and light discing to reduce the compaction of the recipient area. The 0.9 acre parcel was fenced with a split rail around its entire perimeter.

Criteria for Success: None stated in the materials available for review.

Project Success: As of 16 May 1990, 10 of the 12 transplants survived to reproduce and one seedling transplant survived, despite two years of drought. This represents a 90% survival rate for the mature plants. T. Krantz, the contractor from Nativescapes responsible for the transplantation effort, suggests that the project was at least initially successful.

Date Project Initiated: November 1988.

IV.B. Endangered, Threatened, and Rare Plant Species Involved in Research-Related Transplantation, Relocation and Reintroduction Projects

IV.B.1. ***Amsinckia grandiflora*** (Large-Flowered Fiddleneck): State endangered; Federally endangered, CNPS List 1B.

Respondent: Mr. Kevin Shea, East Bay Regional Parks District (EBRPD), Oakland, and data obtained from EPP files.

Project Name and Description: "*Amsinckia Grandiflora* Experimental Reintroduction." EPP contracted with Dr. Bruce Pavlik of Mills College, Oakland, to re-establish *Amsinckia grandiflora* at Black Diamond Mines Regional Reserve, a park within the East Bay Regional Park District (Pavlik 1990). The project included: (1) reintroduction of *Amsinckia grandiflora* to its historic location near Antioch, California ("Stewartville"), (2) monitoring the new population; and, (3) experimentally testing the effects of burning, clipping, and herbicide on survivorship and seed production of *Amsinckia grandiflora.* These results would be used to establish additional satellite populations of *Amsinckia grandiflora.*

Mitigation-Related?: No.

Project Objectives: Establishment of at least four new *Amsinckia* populations within its historic range in order to reduce the probability of extinction.

Project Methods: A 14 x '17 m plot was fenced with barbed wire to exclude livestock. Within the area, 20, 2 x 2 m plots of 4 treatments were selected by a stratified random design. Five plots served as controls, five plots were burned after sowing, five plots were hand-clipped, and five plots were sprayed with a dilute solution of a grass-specific herbicide (fluazifop-p-butyl, known as "Fusilade®", produced by the ICI Corporation).

Amsinckia grandiflora nutlets (3460 total), 1800 from a naturally occurring population (Site 300 source) and 1660 grown at the University of California at Davis were sown on October 19 and 20. Each plot was planted with 160 nutlets by pressing each into a shallow depression in the mineral soil. The nutlets were covered with approximately 20 cc of loose native soil to a depth of 1 cm. No supplements of water or nutrients were applied during the experiment.

Amsinckia grandiflora plots were monitored for the following parameters: (1) germination, (2) stress factors, (3) mortality, (4) phenology, (5) reproductive survivorship,

(6) pin-thrum ratio, and (7) nutlet output per plant and per plot.

Criteria for Success: Not explicitly stated, but the success of the reintroduction effort was based on the result that the maximum nutlet output in the experimental plots exceeded the predicted nutlet output (based on laboratory studies).

Project Success: Pavlik reported the project a success in its first year, based upon the production of approximately 35,000 seeds from 1140 individuals, representing a ten-fold increase over the number (3460) of individuals used in the experiment.

Date Project Initiated: October, 1989

IV.B.2. ***Antennaria flagellaris*** (Stoloniferous Pussytoes): Not state or federally listed, but meets CEQA criteria (§15380?) at the time of transplantation; CNPS List 4.

Respondent: Mr. Gary Schoolcraft, U.S. Bureau of Land Management, Susanville.

Project Name and Description: None. U.S. BLM initiated a transplantation project, moving a portion of a population consisting of approximately 10,000+ individuals, that at the time (1983), was considered the only known population in California. Transplantation was attempted as an experiment because it was believed that gold mining would return to the area, and the population was located at the edge of the previous mining activity.

Mitigation-Related?: No.

Project Objectives: Project was initiated to determine whether transplantation of *Antennaria flagellaris* could be used in the future as mitigation.

Project Methods: Plants were removed in groups from a large (>10,000+ individuals) by shovel. These were then transplanted immediately in flats to the relocation sites. Groups and soils were kept in tact, as much as possible. Some plants were watered with a vitamin B1 mixture, while others were not supplemented. No difference was observed in growth between these two groups.

Each summer following the transplantation, the total number of plants (both live and dead) were counted. No transplanting report was prepared, but internal memoranda describing the transplantation and the concluding activities were prepared. Estimated cost of the transplantation was 1 work day per transplant.

Criteria for Success: Establishment and reproduction of the plants on site, to sufficient numbers to guarantee existence of the population.

Project Success: Not successful. Of the >400 plants transplanted into 4 different populations, only one newly established population exists. This consists of only 17 plants after 6 years. All other died. Schoolcraft suggested that because the plant is a short-lived perennial that reproduces vegetatively primarily by stolons, the receptor site may have had an inappropriate soil texture to allow adequate vegetative reproduction.

Date Project Initiated: October 1983.

IV.B.3. *Arabis macdonaldiana* (MacDonald's Rock Cress): State endangered; Federally endangered; CNPS List 1B.

Respondent: Pardee Bardwell, U.S. Bureau of Land Management (U.S. BLM) and Michael Baad, California State University, Sacramento.

Project Name and Description: "Geographic Distribution of Rare Plants on Public Lands Within the Red Mountain Study Area and A Study of the Population Dynamics and Reproductive Biology of McDonald's Rock-Cress [sic] (*Arabis macdonaldiana*)." The project was contracted by Dr. Baad with the U.S. BLM to determine the: (1) geographic distribution of rare plants on Red Mountain public lands; and, (2) population dynamics and reproductive biology of MacDonald's rockcress (Baad 1987).

Mitigation-Related?: No.

Project Objectives: The overall project objective of the contract was to determine why *Arabis macdonaldiana* is not more widely distributed within the rocky habitats of Red Mountain. The project was initiated in part in response to the 1984 Recovery Plan for

MacDonald's rock cress.

Project Methods: As part of this contract, in November 1985, Dr. Baad planted 30 1 m^2 plots with 100 *Arabis macdonaldiana* seeds each, over a wide range of habitats on Red Mountain. Several plots also received seedlings germinated from seed under greenhouse conditions. These were monitored during 1986.

Criteria for Success: None.

Project Success: The report notes that there was extremely poor germination success by *Arabis macdonaldiana* over the wide range of habitats into which they were outplanted. Dr. Baad concluded that this species has a relatively low rate of germination even in its preferred habitat. Also, the transplants did not do well, surviving in only 3 of the original plots. All but 5 of the original 25 transplants that remained were completely grazed and/or torn out of the ground by herbivores.

Date Project Initiated: Spring 1984.

IV.B.4. *Arctostaphylos hookeri* var. *ravenii* (Raven's Manzanita): State endangered; Federally endangered; CNPS List 1B.

Respondent: Ms. Terri Thomas, U.S. National Park Service, Golden Gate National Recreation Area, San Francisco.

Project Name and Description: "Raven's Manzanita Recovery Plan." The "relocation" project was initiated as part of the Raven's manzanita recovery plan.

Mitigation-Related?: No.

Project Objectives: To expand the number of individuals in the population, so that the single remaining individual could remain undisturbed.

Project Methods: Approximately 60 cuttings were taken and propagated by the Saratoga Horticultural Foundation and the University of California Botanic Garden. Later, 60 plants were outplanted in the Presidio in sites identified as similar to the original serpentine site of the parent plant. Plants were watered periodically throughout the first season. An unreported number of seeds were collected, soaked in concentrated sulfuric acid for three hours, and then washed. They were then stratified in moist peat for three months at room temperature and then for three months in the refrigerator.

Criteria for Success: The criterion for success for the cuttings was simply survival. For the seeds, the criterion for success has not yet been determined, because they are still experimenting with collection times, germination techniques, *etc.* However, no mechanism for protection of the transplants has been initiated.

Project Success: Of the approximately 160 cuttings taken and grown at various local botanical gardens, 60 plants were eventually outplanted. It is not clear from the respondent whether any of these remaining 60 have died, but it appears that they have not.

Date Project Initiated: January 1987.

IV.B.5. *Bensoniella oregana* (Bensoniella): State rare; Federal Candidate C2; CNPS List 1B.

Respondent: Mr. Dave Imper, North Coast Chapter, California Native Plant Society, Eureka.

Project Name and Description: "*Bensoniella* Transplant Project." Project was initiated in 1979 by the Six Rivers National Forest because downcutting of stream channels appeared to threaten populations of *Bensoniella oregana*. Approximately 50 rosettes were removed from the Smokehouse Creek parcel and transplanted to Groves Prairie, east of Willow Creek, in similar habitat.

Mitigation-Related?: No.

Project Objectives: No specific objectives, although generally the Forest Service wanted to prevent the demise of the streamside populations of *Bensoniella oregana*.

Project Methods: Whole plants (rosettes) were removed from the Smokehouse Creek

Parcel (an outholding held by Six Rivers National Forest specifically for *Bensoniella oregana*), and transplanted to Groves Prairie, east of Willow Creek in a similar habitat of white fir (*Abies concolor*)/incense cedar (*Calocedrus decurrens*). Transplants were monitored from 1980-1985.

Criteria for Success: Not clearly defined, other than short-term survival. Respondent noted that a "rather inadequate" measure of vigor was included in the original monitoring plan.

Project Success: Success was not clearly defined, but some rosettes survived. During the first year, a large increase (>100%) in the number of rosettes and inflorescences was observed. However, there has been an apparent failure for these transplants to reproduce sexually. Respondent indicated that so little of the biology of this species is known that it is not clear whether *Bensoniella oregana* reproduces sexually anywhere or whether sexually reproduction is intermittent. Also, respondent indicates that the transplant population has declined significantly within the last year.

Date Project Initiated: 1978-79.

IV.B.6. *Cordylanthus palmatus* (Ferris' Bird's Beak): State endangered; Federal endangered; CNPS List 1B.

Respondent: Dr Larry Heckert, Jepson Herbarium, University of California, Berkeley.

Project Name and Description: None stated.

Mitigation-Related?: No.

Project Objectives: None stated. Presumably the objective of Dr. Heckert was to establish a self-sustaining population of *Cordylanthus palmatus* at the Mendota Wildlife Refuge.

Project Methods: An unspecified number of individuals was collected from somewhere outside the wildlife refuge and transplanted to the refuge. The population lasted for over 10 years, but eventually died out. At some time during this project, a naturally-occurring population was discovered within the Mendota Wildlife Refuge.

Criteria for Success: None stated.

Project Success: Project was successful about a decade, but not for the long term.

Date Project Initiated: late 1970's.

IV.B.7. *Dudleya cymosa* ssp. *marcescens* (Santa Monica Mountains Dudleya): State rare; Federal Candidate C2; CNPS List 1B.

Respondent: Ms. D.A. Hoover, Woodland Hills, California.

Project Name and Description: "Soltice Canyon Native Plant Project." Volunteers from the California Native Plant Society (CNPS) proposed to eradicate invasive exotic species and replace them at Soltice Canyon Park with species native to the Santa Monica Mountains. This project included the reintroduction of *Hemizonia minthornii* and *Dudleya cymosa* ssp. *marcescens*. (see IV.B.8 for more details).

Mitigation-Related?: No.

Project Objectives: Objectives as stated were to expand the protected sites for the relatively rare native species and to learn practical methods for safe propagation without threatening native populations.

Project Methods: Individuals of *D. cymosa* var. *marcescens* were collected (salvaged) from along a road in Red Rock Canyon that was to be graded for fire-break maintenance. Approximately 7-8 individuals were lifted from the hard-packed roadside soil and transplanted to soil-filled pockets on a rocky berm on Humbolt Terrace at Soltice Canyon Park. Each plant was watered by hand for several months. The respondent suggested that the rocky setting protects the plants from gophers and also provides excellent drainage.

Plants were monitored by CNPS members through periodic inspections. Visits included weeding of competing exotics (*e.g.*, castor bean, tree tobacco, mustard, various thistles, *etc.*) and handwatering of additional native species. Total cost of the project was

$130.00 (gas @ $10.00 and paid assistance at $120.00).

Criteria for Success: None stated for *Dudleya cymosa* var. *marcescens*.

Project Success: For *Dudleya cymosa* var. *marcescens*, the respondent felt that the transplantation was successful because the transplanted plants established successfully. However, the respondent also noted that many more individuals of *D. cymosa* var. *marcescens* were lost due to road-scraping. The CNPS hopes to expand this reintroduced population through future off-site seed collection, germination, and transplantation.

Date Project Initiated: 1987; project on-going.

IV.B.8. *Hemizonia minthornii* (Santa Susana Tarplant): State rare; Federal Candidate C2; CNPS List 1B.

Respondent: Ms. D.A. Hoover, Woodland Hills, California.

Project Name and Description: "Soltice Canyon Native Plant Project." Volunteers from the California Native Plant Society (CNPS) proposed to eradicate invasive exotic species and replace them at Soltice Canyon Park with species native to the Santa Monica Mountains. This project included the reintroduction of *Hemizonia minthornii* and *Dudleya cymosa* ssp. *marcescens*. (see IV.B.7 for more details).

Mitigation-Related?: No.

Project Objectives: Objectives as stated were to expand the protected sites for the relatively rare native species and to learn practical methods for safe propagation without threatening native populations.

Project Methods: Seed was collected from two off-site populations in the Santa Monica Mountains (Calabasas Peak and Castro Peak), and stored for several weeks. These failed to germinate, but a second collection was made, and seeds were sown the same day of collection. These seeds germinated and subsequently were transplanted to a screen-covered seed bed in Soltice Canyon Park. The populations were subject to gopher predation and overwatering, however.

Plants were monitored by CNPS members through periodic inspections. Visits included weeding of competing exotics (*e.g.*, castor bean, tree tobacco, mustard, various thistles, *etc.*) and handwatering of additional native species. Total cost of the project was $130.00 (gas @ $10.00 and paid assistance at $120.00).

Criteria for Success: None stated for *Hemizonia minthornii.*

Project Success: Respondent reported that virtually 100% of the seeds germinated, but the very young transplants died from drought. Approximately 10 individuals survived to flower. The Castro Peak seedlings will be transplanted to various locations in the park to test their ability to survive in each (different?) site.

Date Project Initiated: 1987; project on-going.

IV.B.9. *Oenothera wolfii* (Wolf's Evening Primrose): Not California State listed; Federal Candidate C2; CNPS List 1B.

Respondent: Mr. Dave Imper, North Coast Chapter, California Native Plant Society, Eureka.

Project Name and Description: None. Project involved the population expansion within the type locality of *Oenothera wolfii* at Luffenholtz Beach. In December, 1988, 3 individuals of *Oenothera wolfii* were transplanted from Luffenholtz parking area to adjacent habitat, along with two greenhouse seedlings and considerable amounts of seed.

Mitigation-Related?: No.

Project Objectives: The stated objective was to reduce the impacts of repaving, trampling, and vehicular use to populations of *Oenothera wolfii* at Luffenholtz Beach.

Project Methods: Seeds were collected and grown in respondent's greenhouse. Approximately 80 seedling rosettes ranging from 1 - 4 inches in diameter were outplanted on December 26, 1989, in four small areas east of Scenic Drive, south of the residence driveway. In addition, a small amount of seed was planted directly.

Criteria for Success: None stated.

Project Success: Late summer mortality was high. Only 55 seedlings from 7000+ seeds currently survive. Five of the 7 onsite transplants survived, and one of the two greenhouse seedlings. However, the respondent suggests that both seeding and transplantation are potentially viable methods for mitigating impacts on this species, and for expanding small populations.

IV.C. Project Proponents

Of the 46 projects reviewed in this analysis, 17 (37%) were conducted by private businesses involved in housing construction, outdoor recreational facilities, and business offices (Table 4). However, state services such as the California Department of Transportation, California Department of Water Resources, California Department of Parks and Recreation, and the services of two counties (Sonoma and Fresno) together were involved in a total of 15 projects (33%). Finally, an additional 5 projects (11%) were conducted by energy companies (both private and public utilities) (Table 4). The remaining projects were research-related or mitigation-related projects conducted by various agencies of the federal government for a variety of reasons,

V. DISCUSSION OF FINDINGS

V.A. Mitigation Successes

Seven transplantation attempts were considered successful in this analysis. These attempts involved the plant species *Amsinckia grandiflora, Dudleya cymosa* ssp. *marcescens, Holocarpha macradenia, Lasthenia burkei, Opuntia basilaris* var. *treleasei*, and *Sidalcea pedata*. Of these species, the first two were not involved in mitigation-related transplantation efforts. However, the *Amsinckia* project appears to have been so successful because of the great detail and care taken in

TABLE 4. PLANT SPECIES INVOLVED IN TRANSPLANTATION, RELOCATION, OR REINTRODUCTION PROJECTS, PROJECT PROPONENTS, AND DEGREE OF MITIGATION SUCCESS.

SPECIES SUCCESS	PROJECT PROPONENT	PROJECT NAME	PROJECT
Acanthomintha ilicifolia	1) Pardee Company	Westview Planned Residential Development	On-going
	2) Shea Homes	Palos Vista Development	On-going
	3) Pardee Company	Reparation for Sabre Springs Development	On-going
	4) Unknown	Indian Hill, Las Brisas, & Spyglass	Limited success
Amsinckia grandiflora	N/A: Research-Related	*Amsinckia grandiflora* Experimental Reintroduction	Successful
Antennaria flagellaris	U.S. BLM	None	Not successful
Arabis macdonaldiana	N/A: Research-Related	Geographic Distribution of Rare Plants on Public Lands Within the Red Mountain Study Area....	Not successful
Arctostaphylos hookeri var. *ravenii*	N/A: Research-Related	Raven's Manzanita Recovery Plan	On-going
Bensoniella oregana	N/A: Research-Related	*Bensoniella* Transplant Project	Limited success
Blennosperma bakeri	1) Christopherson Homes	Montclair Park	Limited success
	2) Cobblestone Development Corporation	San Miguel Estates	On-going
Brodiaea filifolia	Baldwin Company	College Area Specific Plan in San Marcos	On-going
Brodiaea insignis	Dept. Water Resources	Kaweah Reservoir Dam Expansion	Planning stage
Calochortus greenei	Siskiyou County	None	Not successful
Chorizanthe howellii	UC Davis	None	On-going
Cirsium occidentale var. *compactum*	Calif. Dept. Transportation	Little Pico Bridge Replacement & Piedras Blancas Shoulder widening	Partial success
Cordylanthus palmatus	N/A: Research-Related	None	Partial success
Croton wigginsii	U.S. BLM	None	Not successful
Dudley cymosa ssp. *marcescens*	N/A: Research-Related	None	Successful
Eriastrum densifolium ssp. *sanctorum*	Calif. Dept. Transportation	Santa Ana Woollystar Relocation Project	Not successful
Eriophyllum mohavense	Calif. Energy Commission	LUZ SEGS VII	Not successful
Eryngium aristulatum var. *parishii*	Calif. Dept. Transportation	Caltrans Del Mar Mesa Vernal Pools	Partial success
Erysimum capitatum var. *angustatum*	Pacific Gas & Electric Co.	Vaca Dixon-Contra Costa 230-kV Reconductoring Project....	Partial success
Erysimum menziesii	1) UC Davis	None	On-going
	2) Unknown	Spanish Bay	No information
	3) Unnamed timber company	None	On-going
Erysimum teretifolium	Lone Star Industries, Inc.	Revegetation of Olympia Quarry	Planning stage
Gilia tenuiflora ssp. *arenaria*	Unknown	Spanish Bay	No information
Hemizonia increscens ssp. villosa	Texaco	Gaviota Interim Marine Terminal	On-going
Hemizonia minthornii	1) N/A: Research-Related	None	Not successful
	2) Las Virgenes Municipal Water District	Santa Susana Tarplant Mitigation Program Twin Lakes Tank No. 2	Not successful
	3) Chateau Builders	Woolsey Canyon Development	Planning stage
Holocarpha macradenia	Nylen Company	Hilltop Commons Development	Successful
Lasthenia burkei	1) Unknown	Airport Blvd. Business Park	Successful
	2) Sonoma Co. Airport	Sonoma Co. Airport Expansion	Successful
	3) Cobblestone Development Corporation	San Miguel Estates	On-going
	4) Sonoma County	County of Sonoma Public Service Area 31 Waste Water Storage Pond	On-going
Lilaeopsis masonii	1) Dept. Water Resources	Baker Slough Bank Revetment	On-going
	2) Dept. Parks & Recreation	None	Planning stage
Lupinus tidestromii var. *tidestromii*	Unknown	Spanish Bay	No information
Lupinus milo-bakeri	Calif. Dept. Transportation	None	Unknown

TABLE 4. PLANT SPECIES INVOLVED IN TRANSPLANTATION, RELOCATION, OR REINTRODUCTION PROJECTS, PROJECT PROPONENTS, AND DEGREE OF MITIGATION SUCCESS (cont.).

SPECIES	PROJECT PROPONENT	PROJECT NAME	PROJECT SUCCESS
Mahonia nevinii	RANPAC Corporation	Vesting Tentative Tract No. 23267	Unknown
Monardella linoides ssp. *viminea*	Calif. Dept. Transportation	None	Not successful
Oenothera deltoides ssp. *howellii*	Pacific Gas & Electric Co.	Vaca Dixon-Contra Costa 230-kV Reconductoring Project....	Partial success
Oenothera wolfii	N/A: Research-Related	None	Not successful
Opuntia basilaris var. *treleasei*	1) Calif. Energy Commission	Kern River Cogeneration Power Plant Project	Successful
	2) Sycamore Cogeneration Company	Sycamore Cogeneration Project	Unknown
Orcuttia viscida	Unknown	Sunrise/Douglas Wetland & Creation Program	Ongoing
Pentachaeta lyonii	Unknown	Lake Sherwood Golf Course	Not successful
Pogogyne abramsii	Calif. Dept. Transportation	Caltrans Del Mar Mesa Vernal Pools	Partial success
Pseudobahia peirsonii	Fresno Co. Metro Flood Control District	Round Mountain Flood Control Project	Planning stage
Sedum albomarginatum	Calif. Dept. Transportation	Feather River Canyon Storm Damage Repair	Not successful
Sidalcea pedata	K-Mart Corporation	*Sidalcea pedata* Transplantation Project	Successful

all phases of the research, and that is was peformed by a conscientious and skilled researcher, Dr. Bruce Pavlik. In this instance, the biology of the species was investigated in full, and various relevant (receptor) site treatments were included as an experimental component of the research. It appears crucial that the soil and habitat requirements of the species be understood completely before successful establishment can be assured.

As for the success of the nonmitigation-related transplantation of *Dudleya cymosa* ssp. *marcescens* and the mitigation-related *Opuntia basilaris* var. *treleasei*, these species are succulents which in general, have relatively easy horticultural requirements. Succulents by their biology are rather hardy and tolerant of drought and other forms of disturbance. Therefore, in the case of the Bakersfield cactus, using industry standards for cutting and callus formation may have insured its successful transplantation for the Kern River Cogeneration Power Plant Project. However, the receptor site was also carefully prepared to receive the cactus pads, and this again, appears to be important in assuring success of the transplantation.

The reasons for the success of the thwo *Lasthenia burkei* vernal pool projects (Sonoma County Airport Business Park, and the Sonoma County Airport Expansion are not clear. The issue of vernal pool creation, mitigation, and enhancement is exceptionally contentious among practicing biologists in the State, and there are many differing opinions about vernal pool mitigation "success" (see Ferren and Gevirtz 1990, for example). In a survey such as this, we must accept the accessment of success by the parties responsible for the mitigation, if the established criteria are met and it meets the criteria imposed by this review. In all three cases with *Lasthenia burkei*, populations were established with a greater number of individuals than there present originally (*i.e.*, no individuals). However, because these projects have been on-going for less than 10 years, the long-term viability of the populations is not yet known.

What is also interesting about the vernal pool projects in Sonoma County is that they also involved *Blennosperma bakeri*. Although these projects are technically on-going and were not evaluated as either successful or unsuccessful in this analysis, the early reported results indicate that this species will also successfully establish at created vernal pools. However, one respondent (N. Harrison, San Rosa Jr. College) suggested that despite the purported success of vernal pool creation in Sonoma County, this is an "unsuitable" method for mitigation. Preservation is the only viable mitigation method for vernal pool [plants]. She also reported that Sonoma State University [personnel] has tried for 12 years to vegetate an artificial vernal pool by seeding and transplantation from local sources, but without success. It is not clear from this review why there is such a clear discrepancy in the evaluation of mitigation success for Sonoma County's vernal pool plant species. It is likely that philosophic and ethic differences, rather than biology, drive this debate.

The successful mitigation efforts of the last two species, *Holocarpha macradenia* and *Sidalcea pedata*. are not known. For the Santa Cruz tarplant, the salvage of individual plants was accomplished with care, but preparation of the receptor site was not performed. It is possible that *H. macradenia* is a rather weedy species capable of taking advantage of small site disturbances to establish successfully. As for the bird-footed checkerbloom, the individuals were carefully removed from the construction site, the receptor site was prepared to receive the transplanted individuals, and the receptor site fenced for protection from disturbance. The assessment of success may be premature for this species because the project is only in the second year of monitoring, but the first year survival rate is significant (90%).

V.B. Mitigation Failures

Over one quarter (12 out of the 26 projects; 26%) of the transplantation, relocation, and reintroduction projects in this survey are considered failures. They will not be reviewed individually; however, several are notable, and will serve to illustrate the various reasons for a project's lack of success. The Las Virgenes Municipal Water District's project involving the construction of a water and the consequent destruction of a population of *Hemizonia minthornii* is a controversial mitigation failure that received media attention (Los Angeles Times 1989). Several obvious reasons why this project failed are: (1) seed was collected from plants before it was fully mature (seasoned) and thus subsequent seed germination was poor; (2) plants were collected during the middle of the growing season when they may have been most vulnerable to disturbance; and, (3) because of the nature of the (rock) substrate, individuals were difficult to collect for transplantation. Although an attempt was made to extract individuals carefully, in many cases it appears that the roots had to be broken as individuals were torn from their rock substrate; consequently, few individuals survived.

The difficulties the California Department of Transportation had with the transplantation of *Monardella linoides* ssp. *viminea* again illustrates the problems of native substrate and soils. One of the findings made in the 1986 monitoring report was that this species required its parent material to survive in cultivation. This was discovered after a significant number of individuals had died. For *Antennaria flagellaris*, the respondent suggested that the reason this species did not thrive in its transplantation site was because the soils had an inappropriate soil texture to allow for stoloniferous growth. *Arabis macdonaldiana* is a serpentine endemic, and many such species are difficult to grow in cultivation. Dr. Baad's work demonstrated that this species has poor germination rates even on its native substrate, and did not fare well in any experimental manipulations in the field. Finally, despite serious efforts to control for the unusual edaphic factors that control the distribution of *Eriophyllum mohavense* (and *Chorizanthe spinosa*), transplantation of seeds of the Barstow woolly sunflower and its soil by the California Energy Commission did not succeed. Again, the respondent suggests that the current drought is responsible for the transplantation failure.

Another feature of the mitigation-related transplantation failures is illustrated, again by the California Department of Transportation, in its efforts to transplant *Sedum albomarginatum*. This species is a succulent, and unlike the other succulents in this survey, did not survive its transplantation. It is believed that the transplanted individuals did not survive in large part due to the present drought (Martz, personal communication).

The efforts of the U.S. Bureau of Land Management (BLM) illustrate the problems associated with the transplantation at different life stages. In this instance attempted to transplant seedlings of *Croton wigginsii*. The seedlings were reported as being transplanted with considerable care into an appropriate habitat, but all seedlings died. Because seedlings are a well known to be vulnerable life history stage, manipulations involving seedlings are not likely to succeed.

For other species, such as *Pentachaeta lyonii*, the reasons for failure are not clear. Despite considerable efforts on the part of the consultants to insure mitigation success, including cooperation with the Rancho Santa Ana Botanic Garden for horticultural expertise and sound field methods, the respondent reported that success of the project objectives was not achieved. The reason offered was that the salvage plan was "inadequate."

In summary of the successes and failures of transplantation, relocation and reintroduction of sensitive plant species in California, three broad recommendations can be made that are based on several aspects of the biology of imperiled plant species. These recommendations are:

(1) Individuals should be removed with as little disturbance as possible to the individual, and at a phenologically appropriate time of year when the individual is dormant or photosynthetically inactive;

(2) The receptor site should be of the same habitat quality, particularly with respect to soil

type and its physical characteristics. Various other aspects of the receptor site might include weeding to decrease competition from native and exotic species, watering during times of drought, and fencing and/or other forms of site protection; and

(3) Knowledge of the biology of the organism appears to aid greatly in the design of appropriate horticultural techniques for the preparation of cuttings, transplantation, seed germination, *etc.* This is problematic, however, because the biology of most State-listed species is poorly known. Although some species such as cacti and succulents may be amenable to standard horticultural techniques for propagation, most are not. Therefore, without sufficient knowledge of the biology of impacted species, success of the transplantation, relocation, or reintroduction will not be assured.

V.C. Overview and Summary

Mitigation of impacts to endangered, threatened, and rare plant species is an issue of considerable debate. On the one hand, the Canadian Botanical Association (Fahselt 1988), the American Society of Plant Taxonomists (ASPT 1989), and the Rare Plant Scientific Committee of the California Native Plant Society (CNPS 1990) do not favor mitigation and in point of fact, oppose transplantation as a means of plant preservation except in those instances for which there are no other means of protection. An otherwise doomed population of *Penstemon barrettiae* was transplanted under just such circumstances (Guerrant 1990). Mitigation guidelines propagated by the CNPS (1990) recommend impact avoidance as outlined in the California Environmental Quality Act (CEQA §15370) as the favored mitigation technique.

On the other hand, however, transplantation, relocation, and reintroduction of endangered, threatened, or rare species are routinely performed as mitigation for "unavoidable" project impacts, according to both state and federal environmental legislation. This is currently accomplished in

California for listed plant species through Mitigation Agreements. However, it is remarkable that such potentially harmful activities to State- and (federally-) listed species has, until very recently, been so poorly monitored by all parties (but see new guidelines by Howald and Wickenheiser 1990).

What is equally remarkable is the lack of performance criteria (*i.e.*, criteria for success) of the completed mitigation-related projects reviewed here. Only 15 of the 46 projects (33%) have explicitly defined criteria for success, and until quite recently, there was no consistency in these criteria. Without such "industry" standards, success of translocation, relocation, and reintroduction projects cannot be made objectively. When criteria are explicitly defined, for example the College Area Specific Plan in San Marcos for *Brodiaea filifolia*, mitigation successes can be assessed appropriately.

Such policy statements about transplantation, relocation, or reintroduction as mitigation as those promulgated by the Canadian Botanical Society and the American Society of Plant Taxonomists, combine an ethical viewpoint with a scientific evaluation of plant (and animal) transplantation efforts. For animals, Griffith *et al.* (1989) reported that success rates for the translocation of birds in the United States, Australia, Canada, and New Zealand range widely, from 10% to greater than 90%. The results depended upon the type of animal involved and the conditions of release. They concluded that without high quality habitat at the receptor site, translocations had a low chance of success, regardless of how many animals were released or the condition of the individuals. High quality receptor habitat may be even more critical for plant transplantations than for animals, because of the physical immobility of plants.

For plants, Hall (1986) recently reviewed transplantation for sensitive plants as mitigation for environmental impacts in California, and concluded that transplantation has not been a "panacea" for botanical resource conservation. Hall also suggested that the lack of sufficient post-transplantation maintenance and monitoring has contributed to the unreliability of these mitigation techniques. Monitoring, however, is a labor-intensive commitment, and as such, may not be budgeted appropriately, particularly over the long term. In addition, monitoring of rare plant species can take many forms (see for example, Palmer 1987), and standards for monitoring should be established before mitigation successes can be compared. This is an enormous task.

The effective of many kinds mitigation-related projects is coming into question elsewhere, and it is a critical resource conservation issue for the regulatory community and the public alike. For example, the Florida Department of Environmental Regulation recently issued a report that summarized the success of wetland mitigation required for the issuance of dredge and fill permits under the state Henderson Wetlands Act of 1984 (FDER 1991). The success rate of mitigation was 27% (with some wetland types proving much less successfully mitigated than others). The report also finds that with the institution of simple remedial measures, mitigation success could have been increased to 40% overall. Interestingly, the report documented only 6% (4 out of 63) were found to be in full compliance with the mitigation requirements of the permit.

Some analogies may be relevant here. First, in both instances, success rates for mitigation projects is equal to or less than 25%. This statistic should be unacceptable to the regulating agency, and strongly indicates that the program is not working effectively. Second, some plants (as some wetland habitats) may be more easily manipulated (*i.e.*,, mitigated) than others. This is clearly reflected in the kinds of plants (*e.g.*, succulents and cacti) that were determined to be successfully mitigated in this review. Third, it is likely that with simple remedial measures (as discussed for the Florida wetlands), *e.g.*, hand-watering, weeding of competing exotics, fencing, *etc.*, mitigation success rates for the transplantation of State-listed species could be greatly enhanced. Finally, although not part of this study, it should be investigated whether the permittees are in full compliance with the Mitigation Agreements.

There are some success stories, however. *Stephanomeria malheurensis* (Parenti and Guerrant 1990) and *Styrax texana* (Cox 1990) are two endangered plants that have been successfully reintroduced back into their native habitats in Oregon and Texas, respectively. In many instances, such as these two, success of relocation, reintroduction, or transplantation is achieved through Herculean means. Thus until we understand thoroughly the techniques of translocation, relocation, reintroduction, and restoration, it may be unwise to routinely agree to these forms of mitigation for endangered, threatened, or rare botanical resources.

In conclusion, it is recommended that because of the low success rate of the completed mitigation-related projects involving translocation, relocation, and reintroduction, and the reasonably high number of projects that are on-going and for which no conclusive information is currently available, the Endangered Plant Program should limit their Mitigation Agreements to those projects for which such techniques are the only known means of preservation of a population of an endangered, threatened, or rare species, or for impact avoidance is not possible, and for which there is no demonstrated practicable alternative.

VI. ACKNOWLEDGEMENTS

I gratefully acknowledge all those individuals and organizations who responded to my lengthy questionnaire. In addition, I wish to thank Ann Howald of the Endangered Plant Program for providing me with this opportunity, and for her considerable patience.

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APPENDIX A. EXAMPLE COVER LETTER AND QUESTIONNAIRE

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18 April 1990

Ms. Ann Howald, Program Ecologist
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Dear Ms. Howald:

As part of the California Department of Fish and Game's Endangered Plant Program review of mitigation for state-listed rare, threatened and endangered plant species, I am conducting a survey of mitigation, transplantation, replantation and reintroduction projects that have been implemented or planned in California. The purpose of this survey is to assess the success of mitigation-related transplantation, relocation and reintroduction projects of state-listed plant species.

The enclosed form details fifteen questions. Please answer each to the best of your knowledge. Should you need more room for your answers, please feel free to attach an additional sheet. Copies of any reports for projects of an unusual or special nature, or illustrative for any particular point, would be greatly appreciated.

If you are unable to complete this questionnaire, please contact me at your earliest convenience (415-338-6270). If you would prefer, this questionnaire can be completed by phone if you call me at a time convenient for both parties.

Thank you for your time. Your efforts are of considerable importance for a project that has significant ramifications for the future of the rare plant species of California.

Yours most sincerely,

Peggy L. Fiedler
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Appendix A

APPENDIX B. MAILING LIST FOR QUESTIONNAIRE

Appendix B. Mailing List for Questionnaire

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Woodland Hills, CA 91364

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Tulelake Ranger Station, P.O. Box 369
Tulelake, CA 96134

Rocky Thompson
Curcurt Riders Productions
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Windsor, CA 95492

Robert Thorne
Rancho Santa Ana Botanic Garden
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Claremont, CA 91711

Charlie Turner
1050 San Pablo Avenue
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100 Forni Rd.
Placerville, CA 95667

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Land Restoration Associates
2456 Broadway
San Diego, CA 92101

Julie Vanderweir
Mooney Lettieri & Associates
9903 Business Park Avenue
San Diego, CA 92131

Ricardo Villaseñor
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San Francisco, CA 94103

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650 Capitol Mall
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Sacramento, CA 95825

Jim Wilson
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Rocklin, CA 95677

Tamara Wilton
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Bridgeville, CA 95526

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LTBMU
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Walnut Creek, CA 94598

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Calabasas, CA 91302

Charles G. Wolfe
Kleinfelder
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Sacramento, CA 95814

Patty Worthing
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Walt Wright
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Robert Wunner
Redwood Community Action Agency
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John Zenter
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APPENDIX C. PERSONS RESPONDING TO QUESTIONNAIRE AND SUMMARY RESPONSES

Appendix C. Persons And/Or Agencies Responding to Questionnaire and Summary Responses

Person and/or Agency	Response/Species Involved/Comments
Lowell Ahart Oroville, CA	Never Involved[1]
Bob Allen Larkspur, CA	Never Involved
David Amme Berkeley, CA	Never Involved[2]
Joseph Aparicio Biology Department American River College Sacramento, CA	Never Involved
Wayne Armstrong Department of Biology Palomar College San Marcos, CA	Never Involved
Mike Baad Department of Biological Sciences California State University Sacramento, CA	*Arabis macdonaldiana*
Balance Hydrologics Berkeley, CA [Contact: Barry Hecht]	*Orcuttia viscida*

[1]Never involved refers to the non-involvement of the person, agency or specific branch thereof, in a mitigation-related transplantation, relocation, or reintroduction of a state-listed endangered, threatened or rare species. The party may have been involved in the transplantation of a state- or federally-listed rare, endangered or threatened species, but the project was not related to mitigation.

[2]Mr. Amme reported that he had developed a restoration plan for the Alameda manzanita (*Arctostaphylos pallida*) for the East Bay Regional Park District, but it was never implemented.

Ellen Bauder Dept. Biological Sciences San Diego State University	Never Involved[3]
R.W. Benseler Dept. Biological Sciences California State University Hayward, CA	Never Involved
Albin Bills Department of Biology Butte College Oroville, CA	Never Involved
Charles Black Department of Biology California State University San Diego, CA	Answered with Paul Zedler; *Pogogyne abramsii,* *Eryngium aartistulatum*
Geoff Burleigh San Fernando, CA	Never Involved
California Conservation Corps Sacramento, CA [Contact: Walt Auburn]	Never Involved[4]
California Department of Fish & Game Bishop, CA [Contact: Denyse Racine]	Never Involved
California Department Fish & Game Denair, CA [Contact: Holman E. King]	Never Involved
California Department of Fish & Game Fresno, CA [Contact: Leland K. Ashford, Jr.]	Never Involved
California Department of Fish & Game Grass Valley, CA [Contact: Jeff Finn]	Never Involved[5]

[3]Dr. Bauder sent information on research-related work on San Diego vernal pools.

[4]Recommended contacting others, specifically Chris Sauer at the CCC's nursery.

[5]Mr. Finn mentioned two vernal pool creation/restoration projects near Roseville.

California Department of Fiah & Game Lodi, CA [Contact: Sandy Harrison]	Never Involved
California Department of Fish & Game Marysville, CA [Contact: Dale Whitmore]	Never Involved
California Department of Fish & Game Rancho Cordova [Contact: Response not signed]	*Lilaeopsis masonii*
California Department of Fish & Game Springville, CA [Contact: James V. Crew]	Never Involved
California Department of Fish & Game Endangered Plant Program Sacramento, CA [Contact: Ann Howald]	*Oenothera wolfii* *Sidalcea pedata*
California Department of Fish & Game San Diego, CA [Contact: Denise Racine]	Never Involved
California Department of Fish & Game Yountville, CA [Contact: Carl Wilcox]	*Lasthenia burkei*
California Department of Forestry Jackson State Forest Ft. Bragg, CA [Contact: Dana Cole]	Never Involved
California Department of Parks & Recreation Lodi, CA [Contact: Sandy Harrison]	Never Involved
California Department Parks & Recreation Monterey, CA [Contact: Jean Ferreira]	Never Involved[6]
California Department of Parks & Recreation Sacramento, CA [Contact: Frederica Bowcutt]	*Lupinus tidestromii, Lilaeopsis masonii, Chorizanthe howellii, Erysimum menziesii*
California Department of Parks & Recreation, OHMVR	

[6]Ms. Ferreira mentioned briefly a non-mitigation related project involving *Erysimum menziesii,* but did not send any information regarding the project.

Sacramento, CA [Contact: Roy Woodward]	Never Involved
California Department of Transportation Los Osos, CA [Contact: Gary Ruggerone]	Never Involved[7]
California Department of Transportation Redding, CA [Contact: Sharon Villa]	*Sedum albomarginatum*
California Department of Transportation Sacramento, CA [Contact: Craig Martz]	*Eriastrum densifolium* ssp. *sanetorum* *Sedum albopurpureum*
California Department of Transportation San Diego, CA [Contact: John Rieger]	San Diego Vernal Pool Species
California Department of Transportation San Francisco, CA [Contact: Sid Shadle]	Never Involved
California Department of Transporation Stockton, CA [Contact: Deborah McKee]	Never Involved
California Department of Water Resources Sacramento, CA [Contact: John Squires]	Recommended contacting Phil Wendt re: *Lilaeopsis masonii*
California Energy Commission Sacramento, CA [Contact: James Brownell and Rick York]	*Opuntia basilaris* ssp. *treleasei*[8] *Eriophyllum mohavense*

[7]Mr. Ruggerone sent information on the transplantation work on federal candidate species *Circium occidentale* var. *compactum* in two projects, Little Pico Bridge replacement and the Piedras Blancas shoulder widening.

[8]Neither of these species is state-listed, but *Eriophyllum mohavense* meets CEQA criteria. *Opuntia basilaris* ssp.*treleasei* is a "candidate" for state listing.

California Native Plant Society Dorothy King Young Chapter Gualala, CA	Never Involved
California State Food and Agriculture Sacramento, CA [Contact: Doug Barbe]	Never Involved
Joe Callizo St. Helena, CA	Never Involved
City of Chico Planning Office Chico, CA [Contact: Cliff Sellers]	Never Involved
Curcurt Riders Productions Windsor, CA [Contact: Rocky Thompson]	Never Involved[9]
Katherine Culligan Piedmont, CA	Never Involved
Michael Curto California Deparment of Parks & Recreation San Diego, CA	Never Involved[10]
CWESA Sanger, CA [Contact: Curt Uptain]	Never Involved
Dames & Moore Goleta, CA [Contact: John Gray]	Never Involved
Mary DeDecker Independence, CA	Never Involved
LauraMay Dempster Jepson Herbarium University of California Berkeley, CA	Never Involved
Desert Studies	

[9]Mr. Thompson sent information on a research project involving *Dichanthelium lanuginosum* ssp. *thermale*.

[10]Mr. Curto is no longer with CDPR, and sent personal comments about mitigation-related work with rare plant species.

Fullerton, CA [Contact: Alan Romspert]	Never Involved
Wendie Duron Clovis, CA	Never Involved
EA Engineering Science & Technology Lafayette, CA [Contacts: Sia Morhardt & R. Douglas Stone]	Never Involved
East Bay Regional Park District Oakland, CA [Contact: Kevin Shea]	Never Involved[11]
EIP Associates Sacramento, CA [Contact: Brian Hoffman]	Never Involved
Envicom Corporation Calabasas, CA [Contact: Carl Wishner]	*Pentachaeta lyonii*
Envirosphere Co. Culver City, CA [Contact: David Bradford]	Never Involved
Phyllis Faber Mill Valley, CA	Never Involved
Roman Gankin Redwood City, CA	Never Involved
GENREC Oakland, CA [Contact: Larry Riggs]	Never Involved
Betty & Jack Guggolz Cloverdale, CA	Never Involved
GW Consulting Engineers Citrus Heights, CA [Contact: Jerry Anders]	Never Involved
Nancy Harrison Dept. Life Sciences Santa Rosa Junior College Santa Rosa, CA	Never Involved

[11]Mr. Shea sent non-mitigation related information concerning a research project on *Amsinkia grandiflora* conducted in the EBRPD.

Larry Heckert Jepson Herbarium University of California Berkeley, CA	*Cordylanthus palmatus* *Castilleja uliginosa*
Mary Ann Henry Ridgecrest, CA	Never Involved[12]
Doris A. Hoover Woodland Hills, CA	Never Involved[13]
Barbara Hopper Kenwood, CA	Never Involved
Hydrozoology Newcastle, CA [Contact: Wayne Fields]	Never Involved
J & M Land Restoration Bakersfield, CA [Contact: Diane Mitchell]	Never Involved
Dave Keil Department of Biological Sciences California Polytechnic Institute San Luis Obispo, CA	Never Involved
David B. Kelley Sacramento, CA	Never Involved

[12]Ms. Henry sent comments about her concern over *Eriophyllum mohavense* as potentially threatened.

[13]Never involved in a transplantation, reintroduction or relocation project, but sent information on non-mitigation-related restoration project for *Hemizonia minthornii* and *Dudleya cymosa* ssp. *marcescens*

Kleinfelder Walnut Creek, CA [Contact: Charles G. Wolfe]	Never Involved
L & M Land Restoration Bakersfield, CA [Contact: Diane Mitchell]	Never Involved
Leitner Biological Consulting Oakland, CA [Contact: Barbara Leitner]	Never Involved
The Living Desert Palm Desert, CA [Contact: Jon Mark Stewart]	Never Involved
Los Angeles Department of Water & Power Bishop, CA [Contact: Patti Novak]	Never Involved
Joe McBride Department of Forestry & Resource Management University of California, Berkeley	Never Involved
Niall McCarten Department of Integrative Biology University of California, Berkeley	*Lilaeopsis masonii*
Elizabeth McClintock San Francisco, CA	Never Involved
Malcolm McLeod Dept. Biological Sciences California Polytechnic Institute San Luis Obispo, CA	Never Involved
Dale McNeal Dept. of Biology University of the Pacific Stockton, CA	Never Involved
Jack Major Dept. of Botany University of California, Davis	Never Involved
Jerry Meral Planning & Conservation League Sacramento, CA	Never Involved
Rhonda & Carl Meyers McKinleyville, CA	Never Involved

Maynard Moe Dept. Biology California State University Bakersfield, CA	Never Involved
Gilbert Muth Biology Department Pacific Union College Angwin, CA	Never Involved
Mycorrhizal Services Menifee, CA [Contact: Theodore St. John]	Never Involved
Pacific Gas and Electric Company Department of Engineering Research San Ramon, CA [Contact: Sally deBecker]	Never Involved
Pacific Gas and Electric Company San Francisco, CA [Contact: Frank Chan; Ken DiVittorio]	Never Involved
Pacific Southwest Biological Services, Inc. National City, CA [Contact: Mitchel Beauchamp]	Refused to Answer
V.T. Parker Department of Biology San Francisco State University	Never Involved
Charlie Patterson El Cerrito, CA	*Lasthenia burkei,* *Blennosperma bakeri*
Phillip Williams & Associates San Francisco, CA [Contact: Bob Coats]	Never Involved
Placer County Community Development Dept. Auburn, CA [Contact: Thomas Kubik]	Never Involved
Planning Associates Redding, CA [Contact: Don Burke]	Never Involved[14]

[14] Recommended contacting Dr. Kingsley Stern at Chico State regarding *Orcuttia tenuis*.

Bob Powell Davis, CA	Never Involved
Rancho Santa Ana Botanical Garden Claremento, CA [Contact: Orlando Mistretta]	Indirectly Involved[15]
Thomas Reid Associates Palo Alto, CA [Contact: Taylor Peterson]	Never Involved[16]
Peter Rubtzoff San Francisco, CA	Never Involved
Jake Ruygt Napa, CA	Never Involved
City of Sacramento Planning Dept. Sacramento, CA [Contact: Holly Keeler]	Never Involved[17]
Sacramento County Dept. of Parks and Recreation Sacramento, CA [Contact: Steve Flannery]	Never Involved
Sacramento County Environmental Impact Section [Contact: Doug Peterson]	Never Involved

[15]Provided nursery stock of *Pentachaeta lyonii* to Envicom Corporation, *Acanthomintha ilicifolia* to ERCE, *Cercocarpus traskiae* to the Catalina Island Conservancy, and *Eriastrum densifolium* ssp. *sanctorum* to the U.S. Bureau of Land Management.

[16]Firm was not involved in any transplantation, reintroduction or relocation projects for State-listed species, but did devise a plan for *Castilleja neglecta* that was never implemented due to project postponement.

[17]Ms. Keeler recommended contacting the consulting firm Zentner and Zentner regarding the Laguna Creek Project.

Sacramento County Planning Department [Contact: Robert Burness]	Never Involved
City of San Diego [Contact: Keith A. Greer]	*Monardella linoides* ssp. *viminea*; *Eryngium aristulatum* var. *parishii*[18]
San Diego Department of Public Works San Diego, CA [Contact: Maggie Loy]	Never Involved
Santa Barbara County Santa Barbara, CA [Contact: John Storrer]	*Hemizonia increscens* ssp. *villosa*
City of Santa Rosa [Contact: Denise Peters]	Responded; see Sonoma County Planning Dept.
John Sawyer Biology Department Humbolt State University Arcata, CA	*Erysimum menziesii* *Lilium occidentale*
Marie Simovich Biology Department University of San Diego	Never Involved
James P. Smith, Jr. Dept. Biological Sciences Humbolt State University Arcata, CA	Never Involved
Susan Smith San Francisco, CA	Never Involved
Solano County/ Environmental Management Fairfield, CA [Contact: Karen Wyeth & Cynthia Copeland]	Never Involved
Sonoma County Planning Dept. Santa Rosa, CA [Contact: Ken Milam]	Santa Rosa Plains Vernal Pools

[18]Mr. Greer also sent information for several other plant species that are not state-listed, but have some form of federal status.

Siskiyou County Dept. Agriculture Montague, CA [Contact: Bill Ferlatte]	*Calochortus greenei*
Sonoma State Botanical Garden Sebastopol, CA [Contact: Karen Tatanish]	Never Involved
Sonoma County Planning Department Santa Rosa, CA [Contact: Ken Milam]	*Navarretia plieantha* *Limnanthes vinculans* *Lasthenia burkei*
Stanford University Jasper Ridge Biological Preserve [Contact: Alan Grundman]	Never Involved
John Stebbins Clovis, CA	*Pseudobahia peirsonii*, *Brodiaea insignis*
Sugnet & Associates Roseville [Contact: John Ranlett]	Never Involved
The Nature Conservancy San Francisco, CA [Contact: Robin Cox & Leslie Friedman]	Never Involved
The Nature Conservancy Santa Barbara, CA Peter Schuyler	Never Involved[19]
Tierra Madre Consultants Riverside, CA [Contact: Larry LaPre]	Never Involved[20]

[19]Mr. Schuyler is no longer with The Nature Conservancy.

[20]Tierra Madre Consultants is planning projects that involve the mitigation-related manipulation of *Brodiaea filifolia* and *Eriastrum densifolium* ssp. *sanctorum*.

Tree of Life Nursery San Juan Capistrano, CA [Contact: Mike Evans]	Indirectly Involved[21]
Trust For Public Land San Francisco, CA [Contact: Bennett Johnston]	Never Involved
Tulare County Planning Visalia, CA [Contact: Hector Guerro]	Never Involved
Tuolumne County Planning Dept. Sonora, CA [Contact: John Anderson]	Never Involved
U.S. Army Corps of Engineers Sacramento, CA [Contact: Larry Vinzant]	Never Involved
U.S. Bureau of Land Management Arcata, CA [Contact: Carol Tyson & Steve Hawks]	Never Involved
U.S. Bureau of Land Management Folsom, CA [Contact: D.K. Swickard]	Never Involved
U.S. Department of Energy Sacramento, CA [Contact: No name forwarded on questionnaire]	Never Involved
U.S. Bureau of Land Management Riverside, CA [Contact: Gerald Hillier & Connie Rutherford]	*Croton wigginsii*
U.S. Bureau of Land Management Susanville, CA [Contact: Gary Schoolcraft]	*Antennaria flagellaris*

[21]Mr. Evans forwarded a list of rare, endangered and threatened plants handled by Tree of Life Nursery. State-listed species include: *Acanthomintha ilicifolia, Arctostaphylos imbricata, Brodiaea filifolia, Ceanothus heastiorum, Ceanothus maritimus, Eriastrum densifolium* ssp. *sanctorum, Eriogonum crocatum, Fremontodendron mexicanum, Hemizonia minthornii, Mahonia nevinii, Malacothamnus clementinus,* and *Monardella linoides* ssp. *viminea*.

U.S. Bureau of Land Management Ukiah, CA [Contact: Pardee Bardwell]	*Arabis macdonaldiana* Contracted with M. Baad
U.S. Fish and Wildlife Service San Francisco Bay Wildlife Refuge Complex Newark, CA [Contact: Joy Albertson]	*Erysimum capitatum* var. *angustifolium* ,*Oenothera deltoides* ssp. *howellii*
U.S. Forest Service Alpine, CA [Contact: Maribeth Kottman]	Never Involved
U.S. Forest Service Klamath National Forest Yreka, CA [Contact: Barbara Williams]	*Calochortus greenei*
U.S. Forest Service Lake Tahoe Basin Mgmt. Unit S. Lake Tahoe, CA [Contact: Helen Soderberg]	Never Involved[22]
U.S. Forest Service Modoc National Forest Tulelake, CA [Contact: Laura Thompson]	Never Involved
U.S. Forest Service Pacific Southwest Forest & Range Experiment Station Berkeley, CA [Contact: Connie Millar]	Never Involved
U.S. Forest Service Six Rivers National Forest Eureka, CA [Contact: Dave Imper]	*Bensoniella oregana, Oenothera wolfii*
U.S. National Park Service Channel Island NP Ventura, CA [Contact: Karen Danielson & William Halvorsen]	Never Involved

[22]Never involved in a mitigation-related transplantation, reintroduction or relocation project, but mentioned that the USFS had reintroduced *Rorippa subumbellata* tc three historic locations. No additional information was received.

U.S. National Park Service Golden Gate National Recreation Area San Francisco, CA [Contact: Terri Thomas]	*Arctostaphylos hookeri* var. *ravenii*
U.S. National Park Service Yosemite National Park Yosemite, CA [Contact: Susan Buis]	Never Involved
U.S. National Park Service Monterey, CA [Contact: Robert Branson]	Never Involved
U.S. Navy Public Works Dept. San Diego, CA [Contact: Mike E. Scott]	Never Involved[23]
U.S. Soil Conservation Service Sacramento, CA [Contact: Jack Wright]	Never Involved
University of California Botanical Garden Berkeley, CA [Contact: Holly Forbes]	Never Involved
University of California Hastings Natural History Reservation Carmel Valley, CA [Contact: Susan Schettler]	Never Involved
University of California James San Jacinto Mtms. Reserve Idyllwild, CA [Contact: Michael Hamilton]	Never Involved
University of California Natural Reserves System Oakland, CA [Contact: Norden H. Cheatham]	Never Involved
WESCO Novato, CA [Contact: Diane Hickson]	*Lasthenia burkei*
Western Area Power Administration	

[23]Mr. Scott recommended contacting Zentner and Zentner regarding Miramar.

Sacramento, CA [Contact: Nancy Weintraub]	Never Involved
Williams Enterprises, Inc. Seattle, WA [Contact: Mike Williams]	Never Involved
Vernal Yadon Pacific Grove, CA	Never Involved
Yolo County Resource Conservation District Winters, CA [Contact: John Anderson]	Never Involved
Paul Zedler Department of Biology San Diego State University	Answered with C.A. Black; *Pogogyne abramsii* & *Eryngium aristulatum*
John Zenter Zentner & Zentner Walnut Creek, CA	Called; Never received information on several projects involving *Gratiola heterosepala*, *Sagittaria sanfordii* & *Hibiscus californicus*

Susceptibility of Common and Rare Plant Species to the Genetic Consequences of Habitat Fragmentation

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Abstract: *Small plant populations are more prone to extinction due to the loss of genetic variation through random genetic drift, increased selfing, and mating among related individuals. To date, most researchers dealing with genetic erosion in fragmented plant populations have focused on threatened or rare species. We raise the question whether common plant species are as susceptible to habitat fragmentation as rare species. We conducted a formal meta-analysis of habitat fragmentation studies that reported both population size and population genetic diversity. We estimated the overall weighted mean and variance of the correlation coefficients among four different measures of genetic diversity and plant population size. We then tested whether rarity, mating system, and plant longevity are potential moderators of the relationship between population size and genetic diversity. Mean gene diversity, percent polymorphic loci, and allelic richness across studies were positively and highly significantly correlated with population size, whereas no significant relationship was found between population size and the inbreeding coefficient. Genetic diversity of self-compatible species was less affected by decreasing population size than that of obligate outcrossing and self-compatible but mainly outcrossing species. Longevity did not affect the population genetic response to fragmentation. Our most important finding, however, was that common species were as, or more, susceptible to the population genetic consequences of habitat fragmentation than rare species, even when historically or naturally rare species were excluded from the analysis. These results are dramatic in that many more plant species than previously assumed may be vulnerable to genetic erosion and loss of genetic diversity as a result of ongoing fragmentation processes. This implies that many fragmented habitats have become unable to support plant populations that are large enough to maintain a mutation-drift balance and that occupied habitat fragments have become too isolated to allow sufficient gene flow to enable replenishment of lost alleles.*

Keywords: genetic diversity, habitat fragmentation, inbreeding, mating system, population size

Susceptibilidad de Especies de Plantas Comunes y Raras a las Consecuencias Genéticas de la Fragmentación del Hábitat

Resumen: *Las poblaciones pequeñas de plantas son más propensas a la extinción debido a la pérdida de variación genética por medio de la deriva génica aleatoria, el incremento de autogamia y la reproducción entre individuos emparentados. A la fecha, la mayoría de los investigadores que trabajan con erosión genética en poblaciones fragmentadas de plantas se han enfocado en las especies amenazadas o raras. Cuestionamos si las especies de plantas comunes son tan susceptibles a la fragmentación del hábitat como las especies raras. Realizamos un meta análisis formal de estudios de fragmentación que reportaron tanto tamaño poblacional como diversidad genética. Estimamos la media general ponderada y la varianza de los coeficientes de correlación entre cuatro medidas de diversidad genética y de tamaño poblacional de las plantas. Posteriormente probamos si la rareza, el sistema reproductivo y la longevidad de la planta son moderadores potenciales de la relación entre el tamaño poblacional y la diversidad genética. La diversidad genética promedio, el porcentaje de loci polimórficos y la riqueza alélica en los estudios tuvieron una correlación positiva y altamente significativa*

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con el tamaño poblacional, mientras que no encontramos relación significativa entre el tamaño poblacional y el coeficiente de endogamia. La diversidad genética de especies auto compatibles fue menos afectada por la reducción en el tamaño poblacional que la de especies exogámicas obligadas y especies auto compatibles, pero principalmente exogámicas. La longevidad no afectó la respuesta genética de la población a la fragmentación. Sin embargo, nuestro hallazgo más importante fue que las especies comunes fueron tan, o más, susceptibles a las consecuencias genéticas de la fragmentación del hábitat que las especies raras, aun cuando las especies histórica o naturalmente raras fueron excluidas del análisis. Estos resultados son dramáticos porque muchas especies más pueden ser vulnerables a la erosión genética y a la pérdida de diversidad genética como consecuencia de los procesos de fragmentación que lo se asumía previamente. Esto implica que muchos hábitats fragmentados han perdido la capacidad para soportar poblaciones de plantas lo suficientemente grandes para mantener un equilibrio mutación-deriva y que los fragmentos de hábitat ocupados están tan aislados que el flujo génico es insuficiente para permitir la reposición de alelos perdidos.

Palabras Clave: diversidad genética, endogamia, fragmentación de hábitat, sistema reproductivo, tamaño poblacional

Introduction

Next to decreasing habitat quality and the introduction of exotic species, habitat fragmentation is one of the main drivers behind the present biodiversity crisis (Young & Clarke 2000). Habitat fragmentation includes three components (Andren 1994): (1) pure loss of habitat, (2) reduced fragment size, and (3) increased spatial isolation of remnant fragments. Small habitat fragments contain small populations, which are more vulnerable to extinction due to environmental and demographic stochasticity (Shaffer 1981; Lande 1988). In addition, small populations may be more prone to extinction due to the loss of genetic variation (Frankham 1996). A decreasing population size may result in erosion of genetic variation through the loss of alleles by random genetic drift. In addition, increased selfing (in plants) and mating among closely related individuals in small populations may result in inbreeding and a reduction of the number of heterozygotes (Schaal & Leverich 1996; Young et al. 1996). Over the short term decreasing heterozygosity and the expression of deleterious alleles may result in reduced fitness (Keller & Waller 2002; Reed & Frankham 2003). In the long term lower levels of genetic variation may limit a species' ability to respond to changing environmental conditions through adaptation and selection (Booy et al. 2000).

To date, most studies dealing with genetic erosion in fragmented plant populations have focused on threatened or rare species (e.g., Raijman et al. 1994; Cruzan 2001; Gonzales & Hamrick 2005). The few available studies that explicitly looked for a relationship between habitat fragmentation and genetic erosion in common species, however, have demonstrated that commonness does not protect a species from loss of genetic variation (e.g., Lienert et al. 2002; Hooftman et al. 2004; Galeuchet et al. 2005). These findings are unexpected because common species are by definition characterized by higher fragment occupancy and/or higher local abundance than rare species (Gaston et al. 2000). These spatial population characteristics can be expected to mitigate the loss of genetic diversity in common species, for example, by allowing genetic rescue (i.e., the replenishment of lost alleles through gene flow between habitat fragments) (Richards 2000; Tallmon et al. 2004). On the other hand, rare species include both species that are historically or naturally rare (e.g., Wolf et al. 2000*a*) and those that are rare due to recent population declines. The effects of habitat fragmentation are expected to be more severe in recently fragmented populations (Huenneke 1991; Gitzendanner & Soltis 2000).

If the loss of genetic diversity in common species appears to be a universal phenomenon, then this may have major consequences for plant community composition and species richness of fragmented habitats. In turn, changing community composition and decreasing species richness may negatively affect ecosystem functioning (Loreau et al. 2001; Leps 2005).

Along with rarity, mating system and longevity may also affect the genetic response of plants to habitat fragmentation. Plants display a wide variety of mating systems that differ in their influence on population genetic structure (Barrett & Kohn 1991; Richards 1997). Nevertheless, it is currently not known whether the effects of habitat fragmentation on the degree of inbreeding and genetic drift systematically differ for species with different mating systems and, more specifically, between self-compatible and self-incompatible species (Galeuchet et al. 2005). Longevity (and especially prolonged clonal growth) may also mitigate the loss of genetic diversity because it extends the time between generations and therefore moderates the loss of alleles through genetic drift (Young et al. 1996; Honnay & Bossuyt 2005).

Some authors have compared overall genetic diversity between rare and common (congeneric) species (Hamrick & Godt 1996; Gitzendanner & Soltis 2000) although summary of the available habitat fragmentation studies and comparison of the relationship between genetic diversity and population size between common and rare plant species has not been conducted. Thus, we conducted a formal meta-analysis of habitat fragmentation studies that report the relationship between population size and genetic diversity. Meta-analysis focuses on the size and direction of effects across studies, examining the consistency of effects and the relationship between study features (i.e., moderator variables) and observed effects. We estimated the overall mean and the variance of the correlation coefficients among different measures of genetic diversity and plant population size and tested for rarity, mating system, and longevity as potential moderators of the relation between population size and genetic diversity.

Specifically, we addressed whether small, fragmented plant populations are genetically impoverished compared with larger populations; whether rare species are more vulnerable to habitat-fragmentation-mediated loss of genetic diversity than common species; and how moderator variables mating system and longevity affect the relationship between population size and genetic diversity.

Methods

Study Selection and Coding

In January 2006 we used the keywords *habitat fragmentation AND genetic** in a search of Thomson's on line Web of Science. From this query all papers dealing with plant species and applying codominant markers (allozyme or microsatellite markers) to quantify genetic diversity were selected. Amplified fragment length polymorphism (AFLP) and random amplified polymorphic DNA (RAPD) studies were omitted because we were mainly interested in the effects of habitat fragmentation on the inbreeding coefficient (i.e., on the divergence of observed from expected heterozygosity), which is impossible to infer from dominant DNA markers (Mueller & Wolfenbarger 1999). We supplemented the selected papers with studies we found in the papers' cited literature. We examined the full-text version of all selected studies. Studies that did not report population sizes, the number of samples used for genetic analysis, and genetic diversity measures at the level of the individual population were excluded. Studies dealing with fewer than five populations were also omitted. In two studies we used population density as a surrogate of population size (Neel & Ellstrand 2001, 2003)

In each study we recorded the following measures of genetic diversity for all surveyed populations: inbreeding coefficient (F_{IS}), expected heterozygosity or gene diversity (H_e), percentage of polymorphic loci (P), and the number of alleles per locus (A). Not all studies reported all diversity measures, and in some cases it was possible to calculate the inbreeding coefficient from the reported expected and observed heterozygosity. We recorded the Pearson correlation coefficient (r) between each of the four measures of genetic diversity and population size (number of individuals). In most cases we had to calculate r ourselves. Because the Pearson correlation coefficient quantifies linear fits only, we log transformed population sizes in some cases. This log transformation was not applied more frequently for species defined as common than for species defined as rare. In some studies population sizes were reported as categories. For these cases we calculated the Spearman rank correlation coefficient instead of the Pearson correlation coefficient. The correlation coefficients r between population size and the four genetic diversity measures were used as the effect sizes (ES) of the meta-analysis.

Plant species that were explicitly mentioned by authors as "widespread," "common," or "quite common" were coded as common. Other species, referred to as "threatened," "endangered," "relatively rare," or "rare" were coded as rare. A species could be common in one study and rare in another (e.g., Van Rossum et al. 1997 vs. Van Rossum et al. 2003) or both common and rare in one study. In the latter case the same species was studied in two different regions where it differed in abundance and patch occupancy (e.g., Mandak et al. 2005). We believe that relying on the expert knowledge of the authors on the status of a certain species in a certain region is far more accurate in this context than defining rarity and commonness based on reported population sizes and patch occupancies. Moreover, patch occupancies of the species were rarely reported, and we found no indication that the range in size of the studied populations was different for common versus rare species. This makes a quantitative approach of rarity and commonness extremely difficult. We also coded whether a rare study species was subjected to recent fragmentation events (e.g., Luijten et al. 2000) or whether it was naturally or historically rare (e.g., Wolf et al. 2000*a*).

Almost all studies provided information on the mating system of the study species. This information was always reported as "obligate outcrossing," "self-compatible but mainly outcrossing," or "self-compatible" and was coded accordingly. None of the surveyed species was reported as being a complete selfer. Finally, we recorded whether a species was perennial or annual, and if it was perennial, whether it was reported as being clonal.

Statistical Analyses

The weight of each study was calculated according to Reed and Frankham (2003) as follows: $[(K - 2)N]^{1/2}$, where K is the number of populations in the study and N is the mean number of individuals per population sampled for genetic analysis. The applied weight is, strictly speaking, not equal to the inverse variance of the Spearman rank correlation (K - 3), which is commonly used in meta-analysis (Lipsey & Wilson 2001), but allowed accounting of the number of individuals sampled.

We explored the possibility of a publication bias by examining funnel plots and weighted histograms. Funnel plots were constructed by plotting the ES of each study against study weight. We also calculated the significance of the Spearman rank correlation coefficient between ES and study weight (Light & Pillemer 1984). When authors do not submit studies or editors reject submissions with small treatment effects or nonsignificant results, the literature becomes biased (Thornton & Lee 2000). A publication bias against nonsignificant results implies that only large effects are reported by small sample size studies because only large effects reach statistical significance in small samples. This may result in a positive correlation between ES and study weight.

We performed the meta-analysis according to Lipsey and Wilson's (2001) methods and with SPSS (SPSS, Chicago, Illinois) macros written by these authors. We did not, however, apply the Fisher transformation to the correlation coefficients, because it may lead to overestimation of the ES (Hunter & Schmidt 1990). We preferred to use a more conservative, but more realistic, mixed model with maximum likelihood estimation above a fixed model for calculation of the mean ES (Lipsey & Wilson 2001). Heterogeneity of the ES across studies was examined with the Q statistic (Hedges & Olkin 1985). We tested the role of the moderator variables (commonness, mating system, and longevity) in explaining heterogeneity across studies by performing a one-way analysis of variance (ANOVA) analog mixed model and by examining the resulting Q statistic between groups (Lipsey & Wilson 2001). To test for potential confounding interactions between the moderator variables we measured their pairwise degree of association with a chi-square test. All calculations were performed with SPSS (version 12.0).

Results

The final database contained 57 records, including 52 different plant species covered in 53 publications (Table 1). Twenty-one records applied to common species and 36 to rare species. Nine of these 36 rare species could be defined as historically rare. For two species, no information regarding the mating system could be retrieved. Allozymes were used in all but three studies, and the median number of polymorphic loci was 7 (range 2–21). There was no Spearman rank correlation between any of the four ES and the number of polymorphic loci ($p > 0.1$).

There was no evidence of a publication bias. All four funnel plots were symmetrical around the mean weighted ES (results not shown), and none of the rank correlations between study weight and F_{IS} (0.15), H_e (–0.08), A (−0.13), and P (–0.26) were significant ($p > 0.05$). The mean weighted ES (±SE) for H_e (0.23 ± 0.04), P (0.35 ± 0.05), and A (0.36 ± 0.04) were positive and highly significant ($p < 0.001$), whereas no significant ES was found for F_{IS} (–0.04 ± 0.05).

There were no significant pairwise associations between the three moderator variables ($p > 0.1$). Mean weighted ES for F_{IS}, P, and A were not significantly lower for common than for rare species (Table 2). There was, on the contrary, a trend for a stronger correlation between H_e and population size for common than for rare species (Table 2, Fig. 1). The difference in strength of the ES for F_{IS}, P, and A between common and rare species remained insignificant when the nine historically rare species were omitted from the analysis (results not shown). Mating system did not affect the strength of the correlation between population size and F_{IS}. Self-compatible species, however, showed a lower ES for P, H_e, and A than obligate outcrossers and self-compatible but mainly outcrossing species (Table 3, Fig. 1). Self-compatible species exhibited no significant ES at all (Table 3).

Because only two species were reported to be annuals, we did not conduct a statistical comparison between annuals and perennials. Ten species were considered clonal, but they were not significantly less affected by declining population size than nonclonal species (results not shown).

Discussion

Based on the results obtained for 52 plant species, small populations consistently contained significantly less genetic variation (measured by H_e, A, and P) than large populations. Population size had a lower effect on H_e than on P and A, suggesting that alleles lost through habitat fragmentation and population size reduction were mainly those initially present at low densities (Nei et al. 1975; Sun 1996). Our results support the conclusions of Young et al. (1996) and suggest that loss of alleles through population bottlenecks and random genetic drift play an important role in the genetic impoverishment of plant populations.

Overall, the homozygosity excess, as measured by F_{IS}, was not affected by population size. Heterozygosity can be lost as a direct result of decreasing gene diversity and, more importantly, through increased inbreeding arising from increased self-pollination or mating between related individuals (Barrett & Kohn 1991; Young et al. 1996). Several not mutually exclusive explanations are possible for the absence of an overall relationship between F_{IS} and population size. The F_{IS} in small populations may be biased downward because homozygotes for rare alleles are absent (Kirby 1975; Young et al. 1999), whereas F_{IS} in large populations may be frequently biased upward because of population substructuring (the Wahlund effect) (e.g., Lowe et al. 2004). Moreover, Lesica and Allendorf (1992) suggest that selection against homozygotes occurs during early stages of growth in plant populations.

Table 1. Studies used for the meta-analysis on the relation between genetic diversity and population size.

		Moderator variables[a]			
Species	*Study*	*status*	n	*mating system*	*clonal*
Acacia anomala	Coates 1988	1[b]	10	SC/MO	1
Acer saccharum	Young et al. 1993	0	8	SC/MO	0
Aconitum noveboracense	Dixon & May 1990	1	38	SC	0
Anacamptis palustris	Cozzolino et al. 2003	1	5	SC/MO	0
Antherosperma moschatum	Shapcott 1994	0	22	SC	1
Armeria maritima	Weidema et al. 1996	0	17	OO	0
Arnica montana	Kahmen & Poschlod 2000	1	11	OO	1
Arnica montana	Luijten et al. 2000	1	26	OO	1
Atriplex tatarica	Mandak et al. 2005	0	14	SC	0
Atriplex tatarica	Mandak et al. 2005	1[b]	11	SC	0
Begonia dregei	Matolweni et al. 2000	1	12	SC	0
Begonia homonyma	Matolweni et al. 2000	1	7	SC	0
Brassica insularis	Hutrez-Bousses 1996	1	7	SC/MO	0
Calypso bulbosa	Alexandersson & Ågren 2000	1[b]	21	SC/MO	0
Calystegia collina	Wolf et al. 2000*a*, 2000*b*	1[b]	32	OO	1
Castilleja levisecta	Godt et al. 2005	1	11	OO	0
Centaurea corymbosa	Colas et al. 1997	1[b]	6	OO	0
Clematis acerifolia	Lopez-Pujol 2005	1	9	no data	0
Cochlearia bavarica	Paschke et al. 2002	1[b]	24	OO	0
Erigeron parishii	Neel & Ellstrand 2001	1	31	SC	0
Eriogonum ovalifolium	Neel & Ellstrand 2003	1	31	SC/MO	1
Eucalyptus albens	Prober & Brown 1994	0	25	SC/MO	0
Festuca ovina	Berge et al. 1998	0	34	OO	1
Filipendula vulgaris	Weidema et al. 2000	0	17	SC/MO	0
Gentiana pneumonanthe	Raijmann et al. 1994	1	25	SC/MO	0
Geum urbanum	Vandepitte et al., unpublished	0	18	SC	0
Gymnadenia conopsea	Gustafsson 2000	1	10	SC	0
Gypsophila fastigiata	Lönn & Prentice 2002	0	16	SC/MO	0
Juniperus communis	Oostermeijer & De Knegt 2004	1	12	OO	0
Leontice microrhyncha	Chang et al. 2004	1	6	SC	0
Lychnis flos-cuculi	Galeuchet et al. 2005	0	28	SC	0
Lychnis viscaria	Berge et al. 1998	0	28	SC/MO	0
Lychnis viscaria	Lammi et al. 1999	1	8	SC/MO	0
Megaleranthis saniculifolia	Chang et al. 2005	1[b]	8	OO	0
Microseris lanceolata	Prober et al. 1998	1	16	OO	0
Primula elatior	Van Rossum et al. 2002	0	9	OO	0
Primula veris	Van Rossum et al. 2004	0	24	OO	0
Primula vulgaris	Van Rossum et al. 2004	1	41	OO	0
Rutidosis leptorrhynchoides	Young et al. 1999	1	16	OO	1
Salvia pratensis	Van Treuren et al. 1991	1	14	SC/MO	0
Scabiosa columbaria	Van Treuren et al. 1991	1	12	SC/MO	0
Scuttelaria montana	Cruzan 2001	1[b]	31	SC	0
Silene dioica	Giles & Goudet 1997	0	52	OO	0
Silene nutans	Van Rossum et al. 2003	0	21	SC/MO	0
Silene nutans	Van Rossum & Prentice 2004	0	34	SC/MO	0
Silene nutans	Van Rossum et al. 1997	1	34	SC/MO	0
Silene regia	Dolan 1994	0	18	SC/MO	0
Sorbus aucuparia	Bacles et al. 2004	1	8	OO	0
Spiranthes sinensis	Sun 1996	1	6	OO	0
Stachys maritima	Lopez-Pujol 2003	1	5	SC/MO	1
Succisa pratensis	Vergeer et al. 2003	0	17	SC	0
Swainsona recta	Buza et al. 2000	1	18	SC	0
Trillium camchatcense	Tomimatsu & Ohara 2003	0	12	OO	0
Trillium reliquum	Gonzales & Hamrick 2006	1	21	OO	1
Vincetoxicum hirundinaria	Leimu & Mutikainen 2005	0	12	SC	0
Viola pubescens	Culley & Grub 2003	0	9	SC	0
Washingtonia filifera	McClenaghan & Beauchamp 1986	1[b]	16	no data	0

[a]*Key: status: 1, rare; 0, common;* n, *population size; SC, self-compatible; SC/MO, self-compatible but mainly outcrossing; OO, obligate outcrossing; 1, clonal; 0, not clonal.*
[b]*Naturally or historically rare.*

Table 2. Difference in effect size (ES) between common and rare species (*Q* statistic).

Genetic diversity measure[a]	n	Q *between groups*[b]	*Mean weighted ES by group*[b]	*SE*
F_{IS}	48	0.02		
H_e	51	3.58*		
common	19		0.32***	0.06
rare	32		0.17**	0.05
P	42	0.13		
A	39	0.36		

[a] *Key:* F_{IS}, *inbreeding coefficient;* H_e, *expected heterozygosity;* P, *percent polymorphic loci;* A, *number of alleles per locus;* n, *number of records.*
[b] *$0.05 \le p < 0.1$; **$0.001 \le p < 0.01$, ***$p < 0.001$.

Because in most plant species only a small proportion of the offspring survives into the adult stage, selection against homozygotes may occur without affecting recruitment. Especially under harsh environmental conditions with high selection pressures against homozygotes, heterozygosity may be lost very slowly. For example, in grassland species, highly heterozygous individuals have better survival chances during the gradual process of spontaneous afforestation and subsequent habitat fragmentation (Kahmen & Poschlod 2000). Therefore, the smallest and most fragmented populations do not contain a random sample from previously larger populations; rather they exhibit a significant heterozygosity excess (Raijman et

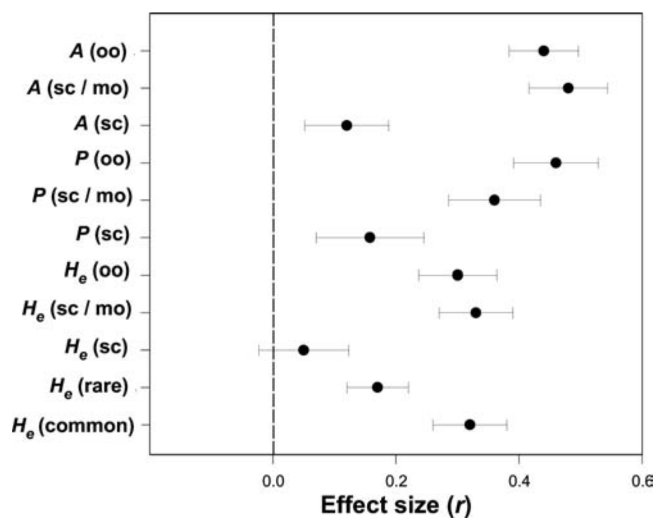

Figure 1. Effect size (correlation between genetic diversity and population size) for 52 plant species considered in 53 publications for the moderator variables with a significant Q *statistic. Bars are standard errors (*H_e*, expected heterozygosity;* A*, number of alleles per locus;* P*, percent polymorphic loci; sc, self-compatible; sc/mo, self-compatible but mainly outcrossing; oo, obligate outcrossing).*

al. 1994; Kahmen & Poschlod 2000). In any case further research regarding the uncertain relation between homozygote excess and plant population size remains necessary, especially because a homozygote excess affects short-term fitness (Reed & Frankham 2003).

Our most important finding was that population genetic diversity (H_e, A, and P) was also eroded in species that were considered common. Even when historically or naturally fragmented populations of rare species were omitted from the analysis, no difference between rare and common species in population genetic response to habitat fragmentation was found. These results are dramatic in that many more plant species than previously assumed may be vulnerable to genetic erosion and loss of genetic diversity as a result of ongoing fragmentation processes. It seems that many fragmented habitats have become unable to support plant populations that are large enough to maintain a mutation-drift balance and that habitat fragments have become too isolated to allow sufficient gene flow to enable replenishment of lost alleles.

Although genetic impoverishment may not result in a short-term loss of fitness in all species, given the absence of a general relationship between population size and F_{IS} (Young et al. 1999; Matolweni et al. 2000), the fragmentation-mediated loss of alleles will at least affect the evolutionary adaptation potential of even common species (Ellstrand & Elam 1993). In the global context of rapid climate change, the latter is alarming because many plant species lack the colonization ability to track the shifting climate northward (Honnay et al. 2002).

Our results also indicated that obligate or mainly outcrossing species are more vulnerable to the loss of genetic variation through habitat fragmentation than self-compatible species. This may be an indication that the role of gene flow is very important in conserving genetic diversity in outbreeding species. Obligate outcrossing or mainly outcrossing species can maintain high population genetic diversity through frequent exchange of genes with other populations and even a very few migrants per generation are sufficient to counter genetic differentiation (Wright 1931). Indeed, these species are generally characterized by low between-population genetic differentiation (Hamrick & Godt 1996). With increasing habitat destruction and decreasing local population size and patch occupancy, the exchange of alleles becomes less likely, and the smallest populations may loose genetic diversity without the possibility of replenishing the alleles lost through drift. Almost all surveyed plant species rely on insects for pollination, and changing pollinator behavior may play an important role in this process (Wilcock & Neiland 2002). Small plant populations may become too inconspicuous or too isolated to attract pollinating insects (Kwak et al. 1998; Steffan-Dewenter & Tscharntke 1999). Increasing fragmentation may therefore directly translate into reduced pollinator activity, reduced gene flow, and loss of genetic diversity. Mainly selfing species

Table 3. Difference in effect size (ES) between different mating systems (*Q* statistic).

Genetic diversity measure[a]	n	Q *between groups*[b]	*Mean weighted ES by group*[b]	*SE*
F_{IS}	46	1.11		
H_e	49	9.97**		
self-compatible	16		0.05	0.07
self-compatible, mainly outcrossing	15		0.33***	0.07
obligate outcrossing	18		0.30***	0.06
P	40	7.62*		
self-compatible	11		0.16	0.09
self-compatible, mainly outcrossing	14		0.36***	0.07
obligate outcrossing	15		0.46***	0.07
A	41	15.84***		
self-compatible	12		0.12	0.07
self-compatible, mainly outcrossing	13		0.48***	0.07
obligate outcrossing	16		0.44***	0.06

[a]*Key:* F_{IS}, *inbreeding coefficient;* H_e, *expected heterozygosity;* P, *percent polymorphic loci;* A, *number of alleles per locus;* n, *number of records.*
[b]*$0.01 < p \leq 0.05$; **$0.001 \leq p < 0.01$, ***$p < 0.001$.*

on the other hand, naturally contain most of their genetic diversity within populations, and their level of population genetic diversity will be less affected by reduced gene flow.

Our inability to find an effect of clonality on population genetic response to habitat fragmentation is likely partly due to the unequal sample sizes between clonal and nonclonal plants. Our results point to a serious bias of plant fragmentation studies toward perennial, nonclonal species. Inclusion of annuals and strongly clonal species in future studies will allow a more accurate assessment of the impact of degree of longevity on the population genetic response to habitat fragmentation.

Some authors suggest that different taxa cannot be treated as independent samples because of their phylogenetic relatedness and that in the absence of a phylogeny only congeneric comparisons can be made (Felsenstein 1985; Gitzendanner & Soltis 2000). We are not aware, however, of any method that includes phylogenetically independent contrasts in a meta-analytical approach, and we found the required habitat fragmentation data for only five congeneric species pairs. Moreover, possible nonindependence of our data increased the probability of a Type I error, making it unlikely that applying a correction for phylogenetic relatedness will reveal significant differences between the response of common and rare species to habitat fragmentation (Gitzendanner & Soltis 2000).

We found a highly significant effect of population size on population genetic diversity, with the exception of the inbreeding coefficient. The population size effect was much more pronounced in self-compatible but mainly outcrossing species and in obligate outcrossing species. Most important, our results revealed that the effect of population size on genetic diversity is as pronounced in common as in rare species. This means that in our fragmented landscapes, even common species may have reached a critical threshold in population size and patch occupancy; thus, measures mitigating habitat fragmentation are strongly needed.

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ENDANGERED MUTUALISMS: The Conservation of Plant-Pollinator Interactions

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ABSTRACT

The pollination of flowering plants by animals represents a critical ecosystem service of great value to humanity, both monetary and otherwise. However, the need for active conservation of pollination interactions is only now being appreciated. Pollination systems are under increasing threat from anthropogenic sources, including fragmentation of habitat, changes in land use, modern agricultural practices, use of chemicals such as pesticides and herbicides, and invasions of non-native plants and animals. Honeybees, which themselves are non-native pollinators on most continents, and which may harm native bees and other pollinators, are nonetheless critically important for crop pollination. Recent declines in honeybee numbers in the United States and Europe bring home the importance of healthy pollination systems, and the need to further develop native bees and other animals as crop pollinators. The "pollination crisis" that is evident in declines of honeybees and native bees, and in damage to webs of plant-pollinator interaction, may be ameliorated not only by cultivation of a diversity of crop pollinators, but also by changes in habitat use and agricultural practices, species reintroductions and removals, and other means. In addition, ecologists must redouble efforts to study basic aspects of plant-pollinator interactions if optimal

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management decisions are to be made for conservation of these interactions in natural and agricultural ecosystems.

INTRODUCTION

To persist on planet Earth, humans depend on "life-support services" provided by biological, geological, and chemical processes in healthy ecosystems. Services such as the cycling of nutrients and regulation of climate are widely recognized. Other such services are less well known, among them biological processes arising from interactions among species, including enhancement of other species' populations by beneficial biotic agents. The pollination of flowering plants is a prime example: Without pollination by animals, most flowering plants would not reproduce sexually, and humans would lose food and other plant products (22).

One measure of the immense value of ecosystem services is monetary value. A recent estimate places a conservative overall mean value per annum of 33 trillion American dollars on all ecosystem services (40); the component due to pollination services is $112 billion. Independent estimates placed the annual value of pollination for crop systems at $20 billion (102) to $40 billion in the United States alone (159); for global agriculture, the estimated value is $200 billion (172). Of pollinators other than honeybees, the value to US crop yields may be as high as $6.7 billion per year (141).

The economic importance of pollination, and its esthetic and ethical values, makes it clear that the conservation of pollination systems is an important priority. In this paper, we describe the ecological and evolutionary nature of plant-pollinator interactions and review evidence that they are increasingly threatened by human activities. We then discuss potential management solutions to ameliorate the "pollination crisis" and highlight areas that call for further research.

THE NATURE OF PLANT-POLLINATOR INTERACTIONS

Modern angiosperms comprise an estimated 250,000 species (81), and most of these—by some estimates over 90% (22, p. 274)—are pollinated by animals, especially insects. Bees alone comprise an estimated 25,000–30,000 species worldwide, all obligate flower visitors (22, 206, 215, 237). The ranks of flies, butterflies and moths, beetles, and other obligate or facultative insect flower visitors surely are several times as large, to which must be added species of birds in several families (35), bats, and small mammals. The number of flower-visiting species worldwide may total nearly 300,000 (141).

Relatively few plant-pollinator interactions are absolutely obligate. Most are more generalized on the part of both plants and animals, and they also vary through time and space (61, 62, 78, 79, 181, 232). For example, the shrub *Lavandula latifolia* in southern Spain is visited by 54 insect taxa from 3 orders, with insects varying substantially in their quality as pollinators (75–77). If added into that is the number of plant species each pollinator visits, the "connectance" of plant and pollinator species in a food web can be high. Jordano (93) reported an average connectance C of about 0.3 for fragments of 36 pollination webs, where C is the realized fraction of the product of n pollinator species and m plant species in the web. C should decline with size of a web, but perhaps not as strongly as previously thought (130, 162).

Recognizing most pollination interactions as being far from obligate fundamentally changes the perception of their conservation. We must abandon the perspective that to lose one plant species is to lose one or more animal species via linked extinction, and vice versa. If the fundamental ecological nature of pollination "interaction webs" is that they are relatively richly connected and shift in time and space, depending in part on the landscape context (20), then the job of conservation biologists is made more subtle and complex.

One major root of generalized interactions is opportunism on the part of both plants and pollinators. To understand this, consider what might be called the fundamental evolutionary nature of pollination. Plants and animal pollinators are mutualists, each benefiting from the other's presence (13; see also 19, 222). But the mutualism is neither symmetrical nor cooperative. Indeed, pollination derives evolutionarily from relationships that were fully antagonistic (44, 167). The goals of plants and animal pollinators remain distinct—in most cases reproduction on the one hand and food gathering on the other—and this leads to conflict of interest rather than cooperation (83, 233, 239, 240). One place to see this conflict is in the behavior of animals such as bees that "rob" flowers for nectar (87).

The conflict of interest dictates that natural selection will act in divergent ways on plants and pollinators. Pollinators are agents of selection and gene flow from the perspective of plants (30) and are involved in evolutionary events ranging from plant speciation to molding floral phenotype. But floral phenotypes are not simply those that are optimal for the animals (84). Conversely, plants select for features of the animal phenotype (200), but the result is not optimal for the plants. The most basic evolutionary outcome that is common across both plants and pollinators is efficiency of each in exploiting what for each is a valuable or critical resource. One common manifestation is opportunism and flexibility on the part of pollinators toward plants, and vice versa.

To devise the best possible strategies for management, conservation, or restoration of pollination systems, it is essential to have several elements in place. We need excellent knowledge of the natural history of plants and pollinators. And we need an appreciation for interaction webs and a "Darwinian perspective" on how natural selection is likely to have shaped behavior, morphology, and other aspects of the phenotype of plants and pollinators.

THE POLLINATION CRISIS

Endangered Pollinators and Plants

Disruption of pollination systems, and declines of certain types of pollinators, have been reported on every continent except Antarctica. Although large regions of each continent have not been evaluated, we can assume that disruption is widespread because the causes are widespread phenomena associated with human activities. The overall picture is of a major pollination crisis (22). The causes include habitat fragmentation and other changes in land use, agriculture and grazing, pesticide and herbicide use, and the introduction of non-native species.

Biological Effects of Fragmentation

Many threats to pollination systems stem from fragmentation of once-continuous habitat. Fragmentation creates small populations from larger ones, with attendant problems that include increased genetic drift, inbreeding depression, and (for very small populations) increased risk of extinction from demographic stochasticity (7, 58, 191). Furthermore, fragmentation increases spatial isolation and the amount of edge between undisturbed and disturbed habitat, both of which can harm pollination (133).

If the isolation of fragmented populations becomes greater than the foraging range of pollinators, if the local pollinator population becomes small enough, or if wide-ranging pollinators avoid small populations, the outcome may be reduced pollination services. Limitation of pollen receipt occurs in many plant species. Burd (23) found evidence for pollen limitation for 62% of 258 species surveyed. The degree of limitation typically varies among years, within a season, among sites within a season, and among plants flowering synchronously within a site (54 and references therein).

Population size contributes to pollen limitation. For example, both male function (pollen removal) and female function (fruit set) are functions of population size for three Swedish orchid species (67; see also 110; see 195 for pollinator visitation rates). Some studies of endangered plants have specifically implicated a lack of effective pollinators. Pavlik et al (152) found that seed set of *Oenothera deltoides* ssp. *howellii* was 26% and 37% of maximum in 2 years and suggested scarcity of hawkmoths as a cause; a related species growing in an unfragmented habitat had seed set that was 65% of maximum. Spatial isolation of plants or populations can also play a role. For example, isolated plants of *Cynoglossum officinale* receive fewer approaches by bumblebees than patches of these plants (108). Percy & Cronk (155) studied an endemic of the island of St. Helena with a total population of 132 adult trees. Pollination is accomplished by small syrphid flies, and pollen delivery declines beyond 50 m; thus, isolated trees are effectively left without pollination.

Pollen limitation does not always imply a dangerous conservation situation. It is often the natural condition due, among other things, to stochasticity in flower visitation (24). Johnson & Bond (92) found widespread pollen limitation in wildflowers in the mountains near Cape Town, South Africa. They attributed this pattern to a general scarcity of pollinators and, in some cases, to lack of floral rewards.

Population size can affect aspects of pollination other than pollen limitation. For example, the composition of the pollinator fauna often differs in flower patches of different size (195, 202). In some cases, such a faunal change may result in higher per-flower visitation rates in small populations (202).

Pollination services are also likely to be affected by density of a plant population, which will sometimes, but not always, covary with population size (114). Thomson (219) and Schmitt (192) reported declines in pollination services at low density for several species in the Asteraceae. Seed set in the desert annual plant *Lesquerella fendleri* depends on the number of conspecifics flowering within 1 m, but not farther away, and behavior of small insect pollinators appears to be the cause (175). Density-related declines in the quality of each pollinator visit (the proportion of conspecific versus foreign pollen delivered) can be more important than parallel declines in the quantity of visits (112, 113, 116).

Interactions of population size, density, and spatial isolation are likely to have even more complex effects on pollination, and these interactions require further study. For example, outcrossing rate is unrelated to population size of an endangered *Salvia* species, but high plant density (in combination with low frequencies of male steriles) promotes outcrossing in hermaphrodites (227). Groom (73) reported that pollen limitation depends on both population size and isolation in a species of *Clarkia*. Of particular concern is an Allee effect—a threshold density, population size, or combination thereof—below which pollinators no longer visit flowers. In a species of *Banksia*, populations below a threshold size produce few or no seeds, presumably in part because of pollen limitation (121; see also 156; for a theoretical approach see 86).

Small plant populations resulting from fragmentation tend to suffer from increased genetic drift and inbreeding depression (58, 228). This may be due to increased geitonogamy, as pollinators may visit a higher proportion of flowers on individual plants, resulting in more self-fertilization (108). Inbreeding depression may explain why small populations of *Ipomopsis aggregata* are more susceptible to environmental stress and have reduced germination success (80). In general, knowledge of the mating systems of plants often is important for conservation. Self-incompatibility may further compound the dangers of small population size by reducing the availability of suitable mates (27, 49, 122).

Studies of Pollination in Fragments

Recent studies illustrate some of the range of fragmentation-related effects on pollination systems. Most of these effects are clearly deleterious. Aizen & Feinsinger (2, 3), who studied habitat fragmentation in dry thorn forest in Argentina, found fragmentation-related declines in pollination, fruit set, and seed set for most of the 16 plant species examined. For at least two species, frequency and taxon richness of native flower-visitors declined with decreasing fragment size, but visitation by introduced Africanized honey bees tended to compensate for loss of visits by natives in small fragments. Honeybees can be successful in disturbed and fragmented habitats (2, 3, 90, 183), and fragmentation may hasten the spread of Africanized bees (2, 3) and the demise of native pollinators (179, 180).

Spears (203) found that pollen dispersal to neighboring plants is significantly reduced in island populations relative to mainland populations of the same species. Pollinator limitation on islands separated by fewer than 10 km from the mainland may foreshadow the fate of many increasingly isolated mainland plant species. For example, seed set in *Dianthus deltoides* declined in habitat islands even though nectar availability was equivalent to that in an undisturbed "mainland" (90).

A few studies have addressed fragmentation and pollination in tropical areas. Powell & Powell (164) used fragrance baits to determine that male euglossine bees, which are pollinators of many neotropical orchids, would not cross cleared areas as small as 100 m between forest habitats. Allozyme heterozygosity, polymorphism, and effective number of alleles decline in small and isolated populations of the tropical tree *Pithecellobium elegans* (74). In seeming contradiction to this apparent genetic erosion in fragments, pollen dispersal by hawkmoths appears to be substantial for this species and seems easily capable of connecting isolated trees and those in fragments to the rest of the population (32).

The generation of new edges as forests are fragmented will change both abiotic and biotic components of the environment. Murcia (138, 139) divided biotic effects into (*a*) direct effects that involve changes in the abundance and distribution of species and (*b*) indirect effects that involve changes in species interactions, including pollination. She detected no consistent changes in pollination levels at a forest edge in Columbia, which suggests that the primary influence of fragmentation is through the creation of smaller populations and the isolation they experience.

The response of insects to fragmentation is poorly understood (50). Bowers (17) studied bumble bee colonization, extinction, and reproduction in subalpine meadows of different sizes. The number and diversity of queens that colonize meadows at the beginning of the summer are positive functions of meadow area, although by mid- to late summer the flower composition of meadows govern species composition and the subsequent reproduction of colonies.

Not all studies have detected negative effects. Stouffer & Bierregaard (209) sampled understory hummingbirds in Amazonian forest before and for nine years after fragmentation. Two species present before isolation did not change in abundance, but one became nearly twice as common, and five were captured only after fragmentation. In contrast to insectivorous birds, the hummingbirds appeared to be plastic in habitat preferences.

Olesen & Jain (144) described how fragmentation can harm not only pollination, but also interactions that plants have with seed dispersers and other mutualists. Loss of these interactions could lead to an extinction vortex with potentially catastrophic consequences for biodiversity. An improved understanding of such effects is critical for conservation (169).

Effects of Agricultural Practices on Wild Pollinators

Humans depend on animal pollination directly or indirectly for about one third of the food they eat (147, 172). Pollination is required for seed production (e.g. alfalfa, clover), to increase seed quality (e.g. sunflower) and number (e.g. caraway), for fruit production and quality (e.g. orchard fruits, melons, tomatoes), to create hybrid seed (e.g. hybrid sunflower), and to increase uniformity in crop ripening (e.g. oilseed rape) (39).

Several features associated with modern agriculture make farms poor habitat for wild bees and other pollinators. Crop monocultures sacrifice floral diversity, and consequently diversity of pollinating insects, over large areas (6, 147, 246). For example, cultivated orchards surrounded by other orchards have significantly fewer bees than orchards surrounded by uncultivated land (193), and the number of bumblebees on crops increases with proximity to natural habitats (246). Chemical fertilizers, pesticides, and herbicides harm pollinators. In addition, marginal land is increasingly cultivated (52, 101, 103, 147, 225 and references therein), resulting in (*a*) loss of wild vegetation to support pollinators, (*b*) fewer areas where bees can nest, (*c*) fewer larval host plants for butterflies, and (*d*) less-varied microhabitats for egg laying and larval development (52, 246). For example, since 1938, Britain has lost 30% of its hedgerow habitats, which provide floral resources and nesting sites for wild bees at the margins of cultivated fields (146).

Elimination of many native pollinators is an unappreciated price that has been paid for increased food production over the last 50 years (172, 224, 225). These pollinators are lost to adjacent natural ecosystems and to crop pollination as well. Although honeybees have long been considered the most important crop pollinators (references in 10, 147), wild pollinators are also important (165) and can be managed to provide "free" services (10, 39, 165).

Shortages of bees to pollinate crops have now been predicted in both Europe and the United States (146, 224). At least 264 crop species from 60 families are grown in the European Union, 84% of which are believed to be dependent on insect pollination (244). The best evidence for declines in bee populations comes from Europe (38, 143, 147, 172, 246), although similar losses have occurred elsewhere.

Damage is not restricted to agricultural situations in industrialized countries. Vinson et al (229) documented disruption in pollination systems following the clearing of tropical dry forest in Costa Rica to provide land for grazing and agriculture. Where livestock are raised, native grasses are commonly replaced with introduced forage grass, which burns more readily and hotly than native grasses. Fires from private lands spread to adjacent forest reserves, threatening native plants and the insects and bats that pollinate most of them. The direct effect of fire is not the only problem. Some specific relationships exist between anthophorid bees such as *Centris* and oil plants of the family Malphigiaceae. Several species of *Centris* depend on finding dead wood with holes formed by wood-boring insects, a resource that disappears when forests are cleared. Many oil-producing plants burn, and those that survive produce less oil. Bees in the dry forests appear to be decreasing in both numbers and diversity, and trees that historically provided bee resources, and depended on bees for outcrossing, are disappearing.

Grazing

Grazing threatens pollinators through removal of food resources, destruction of underground nests and potential nesting sites, and other more subtle mechanisms (70, 96, 211).

Sugden (211) studied sheep grazing practices in California and the effects on pollinators of an endemic vetch (*Astragalus monoensis*) and found evidence of nest destruction, pollinator food removal by sheep, and direct trampling of bees. Bees at risk included *Anthidium*, *Anthophora*, *Bombus*, *Callanthidium*, *Colletes*, *Hoplitis*, and *Osmia*. Another example of removal of food resources by grazing is the loss of willow shrubs (*Salix* spp.) due to cattle along riparian areas. These willows are important browse for livestock (186) and provide nectar and pollen for spring-emerging bumblebee queens and other pollinators; their loss may harm the pollinators and, in turn, other species of plants that flower later in the summer.

Pesticides

Pesticides pose a major threat to pollinators (9). Ironically, the greatest use of pesticides is on crop plants where pollinators are most often limited. Pollinators also are harmed by pesticide application in grasslands (18, 154, 215), forests, (101), urban areas (103), and even tourist resorts (47). An increasing awareness of environmental risks has helped reduce pollinator poisonings in industrialized nations (103), but pesticide-induced declines in bee abundance are still being reported from developing countries (43).

Bee poisoning from insecticides first became a problem in the United States in the 1870s (91), but advances in agricultural technology and elaboration of new chemicals exacerbated the problem after World War II (5, 91). Poisoning of honeybees (on which most attention has been focused) can result in direct mortality, abnormal communication dances, inability to fly, and displacement of queens (91). Foraging honeybees can contaminate the hive with pesticides or other pollutants. Pesticides, arsenic, cadmium, PCBs, fluorides, heavy metals, and radionucleotides (after the 1986 Chernobyl accident) have all been reported in contaminated honey or pollen (103).

In the 1970s, Kevan (98–100) cautioned about the disruptive effects of pesticides on native pollinators, and his predictions have been borne out. The best example is a long-term study conducted in Eastern Canada (99, 101, 103, 104, 106, 161). From 1969 until 1978, spruce budworm was controlled by aerial spraying of Fenitrothion, an organophosphate that is highly toxic to bees. Commercial blueberry production in the region largely depended on pollination by as many as 70 species of native insects. Blueberry crops failed in 1970 and subsequent years (102). Populations of bumblebees and andrenid and halictid bees declined in blueberry fields near sprayed forests (99), and reproduction of native plants was depressed (218, 221). Native bees showed steady signs of recovery after Fenitrothion was replaced with a less harmful insecticide (101).

In the western United States, broad-spectrum insecticides are used to control grasshoppers on rangelands (215). Spraying occurs during the flowering of a number of threatened or endangered endemic plants (18) and coincides with the foraging period of most native bees (154). Spraying is prohibited in a 3-mile radius around points where listed plants are known to occur, but the 3-mile figure is arbitrary because little is known about flight distances of the pollinators (154). Some of these listed species appear to have pollinator-limited seed production (63), and their persistance will be related to successful pollination (194, 215).

Herbicides

Herbicide use affects pollinators by reducing the availability of nectar plants (47, 100). In some circumstances, herbicides appear to have a greater effect than insecticides on wild bee populations (11, 47). Herbicide spraying and mechanical weed control in alfalfa fields can reduce nectar sources for wild bees. The magnitude of the effect for each species is related to the length of its seasonal flight period. Many bees have a flight period that extends beyond the availability of alfalfa flowers. Some of these bee populations show massive declines due to the lack of suitable nesting sites and alternative food plants (11).

Honeybee Declines

More than 9000 years ago, humans realized they could harvest honey from the stores of some bees (69). Humans have taken honeybees with them as they settled new regions of the world (21). Honeybees have been domesticated and naturalized in temperate areas of Australia, North America, and South America for centuries (before 1641 in North America) (196), whereas extensive naturalization in tropical regions is much more recent (183). Although *Apis mellifera* is native to western Asia, it is not widely naturalized in other parts of Asia, where five other species of *Apis* naturally occur (37, 183).

Today, bee products are still valuable, but the value of crop pollination is far greater (22; references in 10). Honeybees, which are generalists and will pollinate many crops, are easily managed and transported (147). Some suggest the annual value of honeybee pollinated crops in the United States alone is as high as $10 billion (235; see also 201, 224).

Recently, honeybees have been declining. More than 20% of the cultivated honeybee colonies in the United States have been lost since 1990 (85, 235), along with most feral honeybees (235). The number of commercially managed colonies has declined from a peak of 5.9 million in the 1940s to 4.3 million in 1985 and 2.7 million in 1995 (85). Declines are severe in some regions. For example, in 1994, California almond growers had to import honeybees from as far away as Florida (235). The European community supports an estimated 7.5 million managed honeybee colonies (244, 245), and these are believed to have been declining since 1985 (245).

Two parasitic mites, *Varroa jacobsoni* and *Acarapsis woodi*, have been particularly damaging to honeybees. *Varroa* spread from its original host, the Asiatic honeybee (*Apis cerana*), when *A. mellifera* was introduced to Asia (57). The mites had spread from Asia to Europe by 1950, to North Africa by 1970, to South America by 1971, and to North America by 1987 (136). A bee infected by *Varroa* loses protein to the parasite, resulting in lowered life expectancy. Also, bacteria penetrate holes in the exoskeleton formed by the mites (174). Existence of *A. woodi*, the tracheal mite, was first documented in England in 1921; subsequently it spread to continental Europe, Asia, Africa, South America, and North America (42, 57). Entire bee colonies become infected, resulting in decreased brood production, decreased honey production, and high winter mortality (48). Beekeepers can attempt to control both mites with chemicals, but *Varroa* mites are beginning to exhibit resistance (236). Treatment can be costly, and chemical residues may appear in honey. New control techniques are being developed, but the difficulty of mite control is causing a decline in beekeeping, particularly among hobbyists (103, 235).

Africanized honeybees also are implicated in honeybee decline in the Americas. The term Africanized has been used to describe hybrids between honeybees of European descent and African subspecies *A. mellifera scutellata* (173). Taylor (214) suggested that the term neotropical African bees be used for the feral colonies in South and Central America that still retain the African phenotype distinguishable by morphology, behavior, and genetics, and that the term Africanized bees be used to refer to bees found primarily in apiaries that show clear evidence of hybridization. The failure to make these distinctions has led to differing predictions about the spread of the bees (214). African queens were released accidently in Brazil in 1956 (136) and rapidly dominated colonies of European descent. The bees became established in the United States in 1990 (22). The predominately African phenotype may be restricted to the warmer climate of the southern United States, but the variable hybrid Africanized phenotypes may be able to survive farther north (214). Neotropical African bees display several features that make them undesirable for apiculture. They swarm when colonies are relatively small and have little honey, and they leave an area when environmental conditions become unfavorable (64). Furthermore, their reputation for aggressive behavior is responsible for negative public attitudes and a decline in beekeeping (22, 34, 201).

Non-Native Pollinators

The introduction of non-native pollinators has the potential to harm native pollination systems. For example, fig wasps were introduced to California in 1899, at which point non-native trees that had been grown there for decades began to produce fruits (51). Because of the introduction of their wasp pollinators, some fig species are now weedy pests in parts of the continental United States, Hawaii, and New Zealand (68, 132). The introduction of bumblebees into areas sometimes have negative results. Non-native *Bombus terrestris* were brought to Japan to pollinate greenhouse tomatoes but soon escaped and became naturalized (I Washitani, personal communication). Because of their aggressive nature, queens are able to take over the hives of native bumblebees by killing the queen, and ecologists fear serious declines in native bumblebee species. Queens of the native Japanese *Bombus diversus* are important pollinators of at least one endangered plant, *Primula sieboldii* (234), and cannot be replaced by *B. terrestris*. *B. terrestris* has also invaded parts of Israel in recent decades, expropriating nectar resources to the apparent detriment of native bees

(46a). *Xylocopa* carpenter bees are pollinators of some plants but are also well known as nectar robbers (87). Little is known about the impact of this bee on native species of flowers or pollinators in Hawaii, where it was introduced (82).

By far the most significant introduction of non-native pollinators involves honeybees, whose movement by humans to all areas of the globe can be considered a major, uncontrolled ecological experiment. Honeybees in some cases might benefit wildflowers by excluding native pollinators from crops (245), but they are often poor pollinators of crops and native flowers compared with native insects (10, 115, 147, 148, 165, 172, 184, 224, 239). Furthermore, honeybee colonies require prodigious amounts of pollen and nectar, and worker bees fly long distances and recruit to rich floral resources (21, 183). Thus, honeybees may compete with native pollinators for resources, leading to reduced species diversity of pollinators. Honeybees also are likely to affect the reproduction of native plants, perhaps even facilitating the spread of weedy non-native plants (4, 8, 82, 128, 188; see also 26). Whether or not honeybees aid in the spread of introduced plants, the presence of these plants may disrupt natural pollination systems because native pollinators sometimes prefer them at the expense of native plants (230).

Competition with honeybees has been implicated in the decline of buprestid beetles in western Australia (109). These jewel beetles are important pollinators in arid mallee scrub vegetation. Sugden & Pyke (212) demonstrated competition by introducing honeybees into an alpine area of Australia and examining the nesting and reproductive success of a generalist native bee. Honeybees remove as much as half of all the available nectar from flowers of the Australian bottlebrush, *Callistemon rugulosus*, and New Holland honeyeaters respond by visiting individual flowers less frequently and expanding their feeding territories (149, 150). Honeybees visit many other Australian plants and on some species remove over 90% of the available resources (151). Roubik et al (176–178, 182, 183, 185) studied competition between African honeybees and native pollinators in South and Central America. In French Guiana, African honey bees are common visitors to *Mimosa pudica* (183). Patches dominated by honeybees had the lowest levels of seed and fruit production, whereas highest levels occurred in patches visited by native *Melipona* bees. Honeybees have been increasing in moderately disturbed, mixed forest-savanna habitats (from 20% of visitors in 1977 to 99% of visitors in 1994), which suggests that they are displacing native insects. Honeybees were introduced onto Santa Cruz Island, off the coast of California, in the 1880s and can now be found foraging on more than one third of the island's plant species (223, 238). Removal of honeybee colonies from the eastern half of the island over the past few years suggests an inverse relationship between honeybee abundance and native bee abundance. Experiments in old field in New York state show that the native megachilid bee *Osmia pumila* suffers reduced brood cell production and pupal mass, and increased brood parasitism in the presence of honeybees (K. Goodall, unpublished).

The hypothesis of competition is not supported by all studies. Sugden et al (213) reviewed 24 studies conducted on four continents and three islands; 16 detected competition under some conditions whereas 8 produced ambiguous results. Although Africanized honeybees reached the neotropics two decades ago and the foraging behavior of native bees changes when honeybees are present, there is no strong evidence of declines in native bee populations (25). Perhaps this is unsurprising: Where honeybees monopolize a rich resource, native species may shift to other flowers and there may be no effect on their population size (150, 183, 190). Also, effects of competition are difficult to detect, if they occur, against the background of natural variation in pollination systems (25, 183). The idea that honeybees automatically compete with natives is probably naive (183), and more studies, including ones of longer duration, are needed.

POTENTIAL MANAGEMENT SOLUTIONS

Conservation of Habitats and Pollinators

Conservation biology is undergoing a paradigm shift away from single-species conservation efforts and toward habitat, ecosystem, and regional efforts. Pollinators should benefit from this change, because the pollinators of many plant species are not yet identified and stand to gain protection from blanket conservation efforts. Also, it is difficult to convince the public to devote resources to protecting small insect pollinators whose aesthetic beauty is not obvious to the unaided eye. The broad context of habitat- or ecosystem-level conservation efforts is especially appropriate for pollination systems because of the web of interactions that links plant species via pollinators (216, 232).

Studies of several systems demonstrate why an ecosystem-based conservation strategy is valuable. A rare orchid in the western United States, *Spiranthes diluvialis*, requires pollinators, so management plans must encompass the maintenance of bumblebees, which may be at risk from insecticide spraying on public rangeland (197). The habitat must also be managed for appropriate nest sites for bumblebees, and for floral diversity to provide nectar (the orchid produces none) and pollen for the whole flight season of bumblebees (199). Petit & Pors (158) calculated the carrying capacity for nectar-feeding bats on the island of Curaçao by using the daily availability of flowers on three species of columnar cacti. They estimated the carrying capacity for one bat species at 1200, about 300 more than the actual population, and suggested that removal of native vegetation on the island should be strictly regulated to prevent further decline. Cropper & Calder (45) attributed the lack of seed set of the rare and endangered Australian orchid *Thelymitra epipactoides* to the absence of pollinators and suggested elimination of natural fire as the root cause. Burning stimulates flowering in many coastal heathland species, which helps to maintain high pollinator species diversity. Kwak et al (118) pointed out the value of other plant species in attracting bumblebees to small populations of the rare Dutch plant *Phyteuma nigrum*.

The dependence of wild pollinator populations on appropriate habitat is increasingly recognized. A study of margins of agricultural fields (119) pointed out that small areas with flowering plants can be very effective at attracting and maintaining pollinator populations, including Syrphidae and other Diptera. Habitat could be managed to encourage bumblebee and honeybee populations by providing a seasonal succession of suitable forage plants, protecting them from pesticides and herbicides and providing for long-term set-aside of fields (38, 145; see also 242). The last recommendation makes sense because butterflies and bumblebees tend to prefer flowers of perennials and because ground-nesting bees avoid recently disturbed areas (38). Such a policy could also benefit insect species that are not crop pollinators, e.g., satyrid butterflies (53).

Conservation of bee habitat may be the best means of reversing declines in pollinator populations (172). In many parts of the world this may mean conservation of human-made habitats, some of which prove to be good substitutes for threatened or destroyed natural habitats (47, 107, 242). Many bee species have colonized restored areas along the Rhine River. Levees can provide prime bee habitat, especially when built of sand and gravel and managed for high floral diversity (107). Day (47) argued that as technology becomes more important and farming starts to decline in Europe, hedgerows, pastures, and woodlands should be regenerated. Disturbed urban areas may also be favorable for some bee communities (189), although multiple types of habitat may be required to satisfy both foraging and nesting requirements (241).

Some pollinators only need a relatively small patch of habitat near their host plants, but others require large areas. In Santa Rosa National Park in Costa Rica, there are at least 40 species of sphingid moths, which pollinate at least 50 plant species as adults and which live for one generation in the park during the beginning of the rainy season before moving to other parts of the country for the rest of the year (89). For these and other migratory pollinators, conservation efforts can require large geographical areas and even international cooperation. Perhaps the most extreme examples are migrants such as hummingbirds, butterflies, and moths, which may be important pollinators along migratory routes extending for thousands of kilometers (12, 28, 71, 231).

Maintenance of Populations and Species in the Absence of Pollinators

Relatively few examples exist of the absolute loss of pollinators, but this may reflect only our ignorance. Steiner (204) reported the loss of a specialized oil-collecting pollinator of a rare South African shrub, although subsequent work (205) led to discovery of a population where the predicted specialist pollinator was still present. Sipes & Tepedino (198, p. 164) suggested that one interpretation of the low visitation and fruit set to a rare plant from the western United States is that the original pollinator "is no longer consistently found within the plants' distribution." Lord (125) described a New Zealand liane that has lost its bat pollinator.

One effort that may, at least in the short term, prove fruitful for conservation is hand pollination of plants that have lost natural pollinators. For example, *Trifolium reflexum*, a prairie species threatened by loss of habitat, was brought into cultivation at the Chicago Botanic Garden, where hand pollination yielded thousands of seeds for additional restoration efforts (208). Hand pollination has also been used for two Hawaiian species of *Brighamia*, whose few remaining individuals have apparently lost their native pollinators (22), and for an endangered orchid in Illinois (168).

Biosphere 2, an experiment in which a small human population was sealed in a (mostly) closed environment for 2 years, included a diversity of plants. All pollinators quickly went extinct so that most plant species "had no future beyond the lifetime of individuals already present" (33). One conclusion is that maintenance of normal plant-pollinator relationships is difficult and that people in such circumstances in the future should be prepared for hand-pollinating.

Another possible solution is the intentional introduction of exotic pollinators, although there are risks (10, 51, 101, 105). The first known example was the introduction of bumblebees to pollinate red clover in New Zealand (51, 65). More recently, weevils were introduced to pollinate oil palms in Malaysia (101), providing services valued at $3 million per year (72, 187).

Changed Agricultural Practices and Uses of Pesticides and Herbicides

In the United States alone, crop production is reduced by about 8000 species of insects, 2000 species of weeds, 160 types of bacteria, 250 types of viruses, and 8000 species of pathogenic fungi (9). Pesticides and herbicides seem an attractive solution because they can rapidly reduce numbers of problem organisms. However, new chemicals must be continually developed as pests evolve resistance and for other reasons (9). One alternative is to move to more labor-intensive control methods that are more "friendly" to pollinators. For example, some USDA studies comparing organic farms and nearby farms using pesticides showed similar crop yields (9). The organic farms controlled pests in ways that encouraged natural predators of pests and created more favorable habitats for pollinators.

There is an increasing emphasis on preventing pollinator loss due to application of crop pesticides. Toxicity levels of pesticides to honeybees are generally known (103), but this has not been useful in determining the effects on other bees (142). Toxicity is in part related to surface-to-volume ratio (91), so that bumblebees may be more tolerant, and small solitary bees more susceptible, than honeybees. In addition, details of pesticide use (such as timing, method of application, and formulation) can affect toxicity (43, 142). Crops can be sprayed before or after flowering to minimize the chances of harming pollinators (66). However, leafcutter bees may collect contaminated leaf tissue for nest construction even when crops are not in flower (142). Timing of application within the day can also be critical. Although honeybees are not active at night, some bees, such as *Nomia*, rest in crop fields at night where they would be susceptible to night spraying (142). Bees such as *Apis* and *Nomia* forage as far as 13 km from the nest (142), so spraying may affect bees that nest far from fields. Honeybee apiaries can be either moved or closed-up during pesticide application, but native bees are not as fortunate. Compounds such as benzaldehyde, propionic anhydride, and some amines may prove useful in repelling bees from fields during pesticide application (142). Bran-baits instead of pesticide spraying could be used to kill grasshoppers in rangelands, thereby potentially reducing pollinator mortality (153).

Few studies have systematically documented declines of bees other than honeybees (but see 99, 103 and references therein). Documentation can be difficult because baseline data are generally unavailable and often the importance of non-*Apis* bees is poorly understood (142). However, enough is known about pesticide problems that much can be done to reduce pollinator losses (103). Kevan (103) suggested regulation and certification for pesticide users. In many countries, regulations are in place but violations carry minimal penalties (103).

Reintroductions of Plants and Pollinators

Reintroduction of endangered plants is still relatively uncommon (60). No plant reintroduction to date appears to have been stimulated by the need to support pollinator populations, although existing pollinators may have benefited. Maunder's (131) paper on plant reintroduction does not mention pollinators, nor does that by Falk et al (60).

One potential problem of reintroducing a plant species into an area is that during its absence some native pollinators may have vanished. This loss would be most serious if the plant had a single pollinator species, but such species appear to be in the minority, and it is common for a plant to have multiple, sometimes very numerous, pollinators (232). Given the variability among years that can be observed in pollinator populations (e.g. 31, 79, 95, 127, 157), multiple pollinators may often be necessary for plant persistence (232).

Hawaii provides one example of an introduction that inadvertently filled the role of a recently extinct pollinator. Cox (41) described the pollination of *Freycinetia arborea*, the indigenous ieie vine, by *Zosterops japonica* (Japanese White-eye, introduced in 1929). Museum specimens of three native birds, two extinct and one endangered, carried pollen grains from the plant, indicating that they were among the original pollinators. Lammers et al (120) reported that White-eyes also visit flowers of an endemic lobelioid, *Clermontia arborescen*. Not all Hawaiian plants have been so lucky; some have gone extinct whereas others are very rare.

Removal of Alien Pollinators

Animals have been intentionally introduced because of their role as pollinators (e.g. honeybees, the alfalfa leafcutter bee). Some intentional introductions involve animals that pollinate but were not introduced for that reason (e.g. *Zosterops* in Hawaii, possums in New Zealand) and some unintentional introductions involve pollinators (e.g. cabbage butterflies, fig wasps). In only a few cases have there been calls for the removal of introduced pollinators. The European bumblebees that were introduced to Japan as pollinators of greenhouse crops escaped to establish feral populations. An effort to eradicate them is underway (M Ono, personal communication). *B. terrestris* was also introduced in about 1992 to Tasmania, where an attempt to eradicate it has had little success (163).

Domestication of Wild Bees and Other Pollinators

Research on non-*Apis* bees as crop pollinators has a long history (15, 224), but it recently has achieved new significance (220, 243). As early as the 1980s, concerns were raised about the need for an increased diversity of pollinators for agriculture in North America (148, 172). At least 50 native bee species have been cultivated experimentally or commercially (43, 172, 224, 225). Parker et al (148) also discussed the use of dipterans as possible crop pollinators.

A few success stories illustrate the potential for non-*Apis* bees as pollinators. The leafcutter bee (*Megachile rotundata*) was introduced from Asia into North America and is the primary pollinator of plants grown to produce alfalfa seed (171, 220). In 1977, *Osmia cornifrons* was introduced from Japan as a pollinator of apples; it has now been distributed to 23 states and 2 Canadian provinces (148; see also 172, 225). In the tomato industry, bumblebees can replace humans equipped with electric vibrators (the flowers require "buzz pollination" to release pollen) or sprayers with synthetic plant hormones to induce fruit production (124, 148, 172). The bumblebee business originated in The Netherlands about a decade ago and has now spread as far as North America and Japan (124, 148, 172).

Legal Protection

Nearly 25% of the planet's vascular plant species may become extinct within the next 50 years (170), and 22% of the species in the United States is currently of conservation concern (59). The situation for most pollinators appears less bleak because the numbers are smaller, but this may only reflect poorer knowledge of them. Both plants and pollinators can be afforded legal protection through the Endangered Species Act in the United States and internationally via listing in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In the United States, only 390 of the 639 species of flowering plants afforded protection by the Endangered Species Act had recovery plans as of December 1997 (http://www.fws.gov/~r9endspp/plt1data.html), and only 16 species of butterflies, 1 species of fly, 1 species of moth, and 2 species of skippers (Lepidoptera) were included in the list as endangered or threatened (http://www.fws.gov/~r9endspp/invdata.html#Insects) as of that date. Three vertebrate pollinators, two flying fox species and the lesser long-nosed bat (*Leptonycteris curasoae*), were also listed as of December 1997. The International Union for Conservation of Nature and Natural Resources (IUCN) now lists 165 genera of vertebrate pollinators (including 186 species) of conservation concern (140), which suggests a need for legal protection for many more.

Public Education

Education efforts have helped bring publicity to bee conservation efforts in Europe, particularly for bumblebees. The Watch Trust for Environmental Education engaged thousands of volunteers, mostly children, to document the abundance and distribution of *Bombus* species and to provide information on preferred plant species (117, 146). The success of this survey inspired a similar program in The Netherlands.

In 1995, The Arizona-Sonora Desert Museum launched the Forgotten Pollinators Campaign. The focus was to draw attention to the impending pollination crisis. The campaign included publication of a book (22), media campaigns, a research program conducted by volunteers, development of pollinator gardens at the museum, and other efforts to increase public awareness of the importance of pollinator conservation.

PRIORITIES FOR FURTHER RESEARCH

In virtually all cases, biologists must provide scientific information for conservation decisions based on less-than-perfect knowledge. The best approach is to base scientific input on the consensus of experts; this is vastly preferable to no scientific input at all or to that of a small minority (55). At the same time, it is important for pollination biologists to map out a research program for filling major gaps in our knowledge, as we attempt to do here.

The Ecology of Animal Pollinators

Typical ecosystems at intermediate latitudes harbor as many as several hundred pollinating insect species, most belonging to Hymenoptera, Lepidoptera, Diptera, and Coleoptera (79, 111, 134, 157, 210, 247). The vast majority of hymenopteran pollinators are solitary bees (237). Compared with our understanding of social bees, we still have much to learn about the nesting biology, demography, and trophic ecology of most solitary bees and about the composition of local species assemblages (137, 215). Relative abundances of given species of solitary bees fluctuate spatially and temporally (31, 157), and we need to understand how this relates to floral resources (215). We also need to learn more about the degree of specialization of individual bee species and the degree to which even specialists may use other plant species (31, 46). The picture for other insect orders is further complicated by the fact that larvae may require food plants that differ from those of adults. We need to learn how to manage landscapes that will support the entire life cycle of such species (22, 14). Our knowledge of larval ecology is best for the Lepidoptera because of the intense interest of naturalists in butterflies (56). More effort needs to be expended in learning comparable information about dipteran and coleopteran life cycles and larval diets. The role of flies as pollinators in many ecosystems seems to have been underestimated until recently (94, 157, 226, 247).

Links Between Pollination and Plant Population Dynamics

The diversity of pollinators is matched by local diversity of plant species and temporal and spatial variation in species composition. For example, Tepedino & Stanton (217) reported substantial year-to-year variation in relative abundances and phenologies of different flowers in a shortgrass prairie in Wyoming (see also 88, 166). Thus, a pollinator foraging for floral reward experiences a complex and fluctuating marketplace. It is important to characterize variation in floral abundance more carefully and to study how pollination contributes to it. Ecologists have assumed that pollination plays an important role in plant population dynamics, but there is virtually no empirical evidence for it. We do know that pollination is often limiting to seed production (23), although resources (207) or both pollination and resources simultaneously (29, 135) can also be limiting. However, we need more experimental manipulations of seed input, seedling establishment, and other stages of the life cycle with measurement of subsequent changes (if any) in plant population size and structure (1, 126, 129).

In particular, it would be useful to design such studies so they help us to predict how reduction in pollination services will influence the demography of plant species that are threatened because of fragmentation of other anthropogenic insults.

The Nature of Interaction Webs

Pimm (160) distinguished four aspects of ecological stability, one of which is resilience—the degree to which an ecosystem resists further change following initial change. Pollination webs are threatened with the loss of component species and addition of non-natives. The substantial connectance of pollination webs makes us suspect that such changes will elicit additional ones, perhaps even cascades of extinction. To our knowledge, nobody has modeled resilience (or other aspects of stability) specifically for mutualistic interactions such as those of plants and pollinators, much less studied resilience of such systems empirically.

CONCLUDING THOUGHTS

The natural history knowledge of pollination gained over the last several centuries shows that animal-mediated pollination is essential for the sexual reproduction of most higher plants. Although many plants are iteroparous, with multiple opportunities for sexual reproduction, spread by clonal propagation or other asexual means or having a dormant seed stage, these life-history features cannot compensate in the long term for a chronic loss of pollination services (16). A reduction in plant fecundity is of clear concern for agroecosystems but equally problematical for natural ecosystems. There is indeed a strong argument to be made that pollination interactions are keystones in both human-managed and natural terrestrial ecosystems (102).

In spite of centuries of study, our understanding of interactions between plants and animal pollinators is far from complete. Appreciating this was our motivation for stressing that continued research is essential to the long-term conservation of pollination systems. At the same time, we agree with others in political and scientific circles who urge ecologists to become more active in educating those around them about issues in conservation biology. The evidence on multiple fronts is sufficiently alarming to conclude that there is an ongoing and pending ecological crisis in pollination systems. Although there are dangers in sounding the alarm for a pollination crisis, and hurdles to be overcome in explaining the issues to a wider audience, the alternatives hold far greater risks.

Our understanding of the keystone role that pollinators can play in ecosystems around the world, and the risks faced by both pollinators and the plants they visit, has increased greatly during the past few decades. Research on endangered plants, including rehabilitation and reintroduction programs, is more likely now than in the past to include consideration of breeding systems and the potential need for pollinators in management plans (97, 123). The conservation of insects and their habitats is now a topic for discussion in the scientific literature (36). A decade ago, Feinsinger (62) found only two papers that clearly related conservation and animal-flower interactions; now these topics are written about frequently, as our review shows. Much progress has been made since Kevan's plea arising from concern about the damage to pollinators from pesticide and herbicide use in Canada (100). The most encouraging progress is that we now recognize much more clearly what problems exist and what we need to know to solve them.

At the same time, many challenges lie ahead. We must redouble our research efforts on basic aspects of pollination systems at a time when it is difficult to obtain financial support for work that lacks immediate management applications. The pace of change in ecosystems and growth of threats to pollination systems promise to increase in the future. We face accelerated alteration of habitat by a growing human population, linked with accelerated invasion of non-native species, and the prospect of global climate change, which threatens to decouple plants and pollinators phenologically and ecologically (166). Although the challenges are daunting, they must be met with our most determined efforts as ecologists and citizens.

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Rapid Genetic Decline in a Translocated Population of the Endangered Plant *Grevillea scapigera*

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Abstract

Grevillea scapigera is one of the world's rarest plant species, currently known from only five plants in the wild. In 1995, 10 plants were selected from the 47 plants known at the time to act as genetically representative founders for translocation into secure sites. Ramets were micropropagated and introduced into one of these secure sites (Corrigin) in 1996, 1997, and 1998. By late 1998, 266 plants had been successfully translocated and were producing large numbers of seeds. With the development of an artificial seed-germination technique and because of an absence of seed germination in situ, seed was collected from these plants and germinated ex situ, and 161 seedlings were returned to the field site in winter 1999. We used the DNA fingerprinting technique of amplified fragment-length polymorphism (AFLP) to (1) assess the genetic fidelity of the clones through the propagation process, (2) contrast genetic variation and average genetic similarities of the F1s to their parents to assess genetic decline, and (3) assign paternity to the reintroduced seeds to assess the reproductive success of each clone. We found that 8 clones, not 10, were present in the translocated population, 54% of all plants were a single clone, and the F1s were on average 22% more inbred and 20% less heterozygous than their parents, largely because 85% of all seeds were the product of only 4 clones. Ultimately, effective population size (N_e) of the founding population was approximately two. Our results highlight the difficulty of maintaining genetic fidelity through a large translocation program. More generally, rapid genetic decline may be a feature of many translocated populations when N_e is small, which may ultimately threaten their long-term survival Strategies to reverse this genetic decline include equalizing founder numbers, adding new genotypes when discovered, optimizing genetic structure and plant density to promote multiple siring and reduce kinship, promoting natural seed germination in situ rather than artificially germinating seeds ex situ, and creating a metapopulation of numerous translocated populations to restore historical distribution patterns and processes.

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Population size and the risk of local extinction: empirical evidence from rare plants

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Matthies, D., Bräuer, I., Maibom, W. and Tscharntke, T. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. – Oikos 105: 481–488.

Due to habitat fragmentation many plant species today occur mainly in small and isolated populations. Modeling studies predict that small populations will be threatened more strongly by stochastic processes than large populations, but there is little empirical evidence to support this prediction for plants. We studied the relationship between size of local populations (number of flowering plants) and survival over ten years for 359 populations of eight short-lived, threatened plants in northern Germany (*Lepidium campestre*, *Thlaspi perfoliatum*, *Rhinanthus minor*, *R. serotinus*, *Melampyrum arvense*, *M. nemorosum*, *Gentianella ciliata* and *G. germanica*). Overall, 27% of the populations became extinct during the study period. Probability of survival of a local population increased significantly with its size in all but one species (*R. minor*). However, estimated population sizes required for 90% probability of survival over 10 years varied widely among species. Survival probability increased with decreasing distance to the nearest conspecific population in *R. serotinus*, but not in the other species. The mean annual growth rate of surviving populations differed greatly between species, but was only for *G. germanica* significantly lower than 1, suggesting that there was no general deterministic decline in the number of plants due to deteriorating habitat conditions. We conclude that the extinction of populations was at least partly due to stochastic processes. This is supported by the fact that in all species a considerable proportion of small populations survived and developed into large populations.

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Habitat fragmentation is one of the main threats to biodiversity. Because of the destruction and fragmentation of habitats many species today occur mainly in small and isolated populations, which for a number of reasons are expected to face a high risk of extinction. In small patches habitat quality may deteriorate (Oostermeijer et al. 1994a) and modelling studies suggest that small populations will be particularly vulnerable to the effects of demographic, environmental and genetic stochasticity (Goodman 1987, Menges 1991a). While demographic stochasticity is only a threat to very small populations, environmental stochasticity has been identified as the most important factor threatening extinction to fragmented populations (Lande 1993, Wissel and Zaschke 1994, Menges 1998, Holsinger 2000).

Predicted genetic consequences of small population size are increased inbreeding, loss of genetic variation due to genetic drift and the accumulation of deleterious mutations ("genetic erosion", Ouborg et al. 1991, Young et al. 1996, Dudash and Fenster 2000). In the short term, genetic erosion may result in a decline of individual fitness and in the long term in a loss of evolutionary

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flexibility, which may decrease the potential for a population to persist in the face of environmental change (Huenneke 1991, Ellstrand and Elam 1993). Genetic variability in small plant populations is often reduced (van Treuren et al. 1991, Ellstrand and Elam 1993, Fischer and Matthies 1998a) and some studies have also found a reduced performance of offspring and lower plasticity (Menges 1991b, Oostermeijer et al. 1994a, Fischer and Matthies 1998b, Kéry et al. 2000).

Moreover, in small populations important interactions with mutualists like pollinators and seed dispersers may become disrupted (Kearns et al. 1998). Because plants in small and isolated patches receive fewer visits from pollinators, fecundity may be reduced due to insufficient pollination (Lamont et al. 1993, Ågren 1996, Groom 1998, Steffan-Dewenter and Tscharntke 1999). Pollen quality may also be lower because in small patches pollination will often be between close relatives. In self-incompatible species reproduction may be reduced in small populations due to a lack of incompatibility alleles (Byers 1995) and in heterostylous species because of unequal morph ratios (Kéry et al. 2003).

The negative effects of fragmentation on reproduction and on the performance of offspring should affect the dynamics and survival of populations of short-lived species relatively quickly, because population persistence depends on frequent recruitment. In contrast, in long-lived species the negative consequences of reduced population size and increased isolation may not become visible for a long time, because established plants often have low mortality (Oostermeijer et al. 1994b, Colling et al. 2002).

With respect to the conservation of biodiversity the most important question is what combined effect the various negative effects of reduced population size have on the persistence of populations. It has been suggested that populations reduced below a certain threshold number of individuals may enter a so called extinction vortex, i.e. a downward spiral of ever decreasing population size and plant fitness that may drive a population to extinction (Gilpin and Soulé 1986, Lamont et al. 1993). However, while there is some direct empirical evidence from animal studies for the negative effects of small population size on the survival of local populations (Pimm et al. 1988, Berger 1990, Thomas 1994a, Lima et al. 1996, Krauss et al. 2003), little such evidence exists for plants. Empirical studies require long-term data on the dynamics and survival of populations which are rarely available for plants. Previous studies have therefore used substitutes for population size like site area (Ouborg 1993) or mean cover (Fischer and Stöcklin 1997).

In an exceptional programme, the distribution and size of the populations of all endangered plant species had been recorded in the mid 1980s in the state of Lower Saxony in northern Germany (Garve 1994). We re-visited 359 populations of eight short-lived endangered plants ten years later, recorded the number of individuals and used the data to analyse the relationship between the size of local plant populations and their probability of survival. We were also interested in the population size required for survival of populations of the various species. In addition, we studied the mean population growth rate of surviving populations to detect a possible general deterministic decline of species and asked whether there was evidence for extinction vortices, i.e. whether small populations were doomed to become extinct.

Material and methods

For the study we selected eight short-lived species which are endangered in northern Germany (Garve 1994) and whose populations are concentrated in southern Lower Saxony: *Lepidium campestre* (L.) R. Br, *Thlaspi perfoliatum* L. (Brassicaceae), *Rhinanthus minor* L., *R. serotinus* (Schönh.) Oborny, *Melampyrum arvense* L., *M. nemorosum* L. (Scrophulariaceae) and *Gentianella ciliata* L. Borkh. and *G. germanica* (Willd.) Börner (Gentianaceae). The *Rhinanthus* spp., *Melampyrum* spp. and *T. perfoliatum* are annuals, *Lepidium campestre* is annual or biennial, *G. germanica* is a biennial and *G. ciliata* has been classified as both a biennial and a perennial (Kutschera and Lichtenegger 1982–1992, Jäger and Werner 2002, Oberdorfer et al. 2002). We selected short-lived plants for the study, because in these species population turnover and extinctions should be most pronounced.

The studied plants have no clonal growth and are propagated only by seeds. All species had populations in calcareous grasslands, but the main habitats of *M. nemorosum* are the margins of woodlands (Matthies 1991) and most populations of *L. campestre* are found at waysides and in old quarries (Bräuer, unpubl.). As part of the plant assessment programme of the state of Lower Saxony, data on the exact location of all populations of rare and endangered plants in Lower Saxony had been recorded since 1982, together with an estimate of the size of populations (Garve 1994). The number of individuals (flowering plants) in each population had been recorded in eight classes (1, 2–5, 6–25, 26–50, 51–100, 101–1000, 1001–10 000, 10 001–100 000 individuals).

In 1996, based on the old records, 359 populations of the study species (36–54 for each species) in southern Lower Saxony were selected for the study. Care was taken to select for each species a balanced sample of populations of different size. Sites that had obviously been destroyed or strongly disturbed were excluded. In summer and autumn 1996, at the time of peak flowering of the study species, all selected sites were visited and an extensive search for the plants was carried out. If individuals of the study species were still present, the number of flowering plants was recorded. For each population the distance to the nearest population was determined from a map.

We used logistic regressions to relate the presence and absence of the species at a site to population size in the mid-1980s and the distance to the next population. The mean recording year was 1986, so we will always refer to 1986 in the following. For the analyses, the geometric mean of the upper and lower boundaries of the old size classes was used as an estimate of population size. Backward elimination based on likelihood ratios was used to derive a model that contained only significant predictors. If population size had a significant effect on population survival, the regression was used to calculate the population size necessary for a 90% probability of survival over 10 years. This is an estimate of a minimum viable population size (Menges 2000) and serves as an overall indicator of a species' sensitivity to fragmentation. We used a 90% rather than a 95% probability of survival because errors strongly increase near the upper limit of survival values.

Mean annual growth rates for the surviving populations were calculated as $\lambda = (\text{population size in 1996/ pop. size in the mid 1980s})^{1/n}$, where n is the number of years between surveys. Differences among species in mean annual growth rate were tested by analysis of variance and deviations of growth rates from 1 (i.e. no change in population size over time) were analysed with t-tests. All analyses were carried out with SPSS for Windows 10.0.

Results

Overall, 73% of the study populations that had been present in 1986 still existed in 1996. The proportion of surviving populations varied among the eight species ($chi^2 = 13.7$, $df = 7$, $p = 0.057$). While 84% of the populations of *R. minor* had survived, only 56% of those of *L. campestre* still existed (Table 1).

Pooled over all species, large populations had a much higher chance of survival than small populations ($chi^2 = 67.0$, $df = 7$, $p < 0.001$). Most of the populations consisting of less than 6 plants in 1986 did not survive until 1996, whereas 100% of those with more than a 1000 individuals survived (Fig. 1). The relationship between population size and survival in the individual species was analysed by logistic regression. In seven out of the eight studied species the probability of survival of a population significantly increased with its size (Fig. 2, Table 1). Only in *R. minor*, the species with the smallest decline in the number of populations, no significant relationship between population size and probability of survival was found ($p = 0.29$), but the logistic regression coefficient had the expected sign. However, there was large varia-

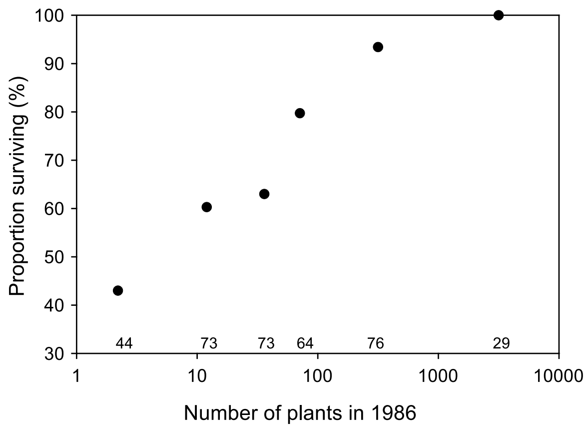

Fig. 1. The relationship between the size of a plant population in 1986 and its probability of survival until 1996. Data were pooled over all eight study species. To achieve sufficient samples sizes, data for populations with less than 6 flowering plants were pooled and the one population with more than 10 000 individuals was pooled with those of the next smaller size class. Numbers denote the number of populations in the respective size category.

Table 1. Proportion of populations surviving from 1986–1996 and logistic regression equations relating survival probability to population size for eight rare plant species in Northern Germany. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. The probability of survival is given by $e^{\text{linear predictor}}/(1 + e^{\text{linear predictor}})$. In the linear predictor, $x = \log_{10}$ (population size) and $y = \log_{10}$ (distance to the nearest population in km). The distance to the nearest population had a significant effect ($chi^2 = 5.8$, $p < 0.05$) only in *Rhinanthus serotinus*. $N_{90\%}$ gives the calculated population size necessary for a 90% probability of survival over 10 years. $N_{90\%}$ was calculated as $10^{[\ln(0.9/0.1) - a]/b}$, where a and b are the constant and the slope parameter from the linear predictor, respectively.

Species	Proportion surviving (%)	Linear predictor	Model chi^2	n	$N_{90\%}$
Lepidium campestre	56	$-2.11+2.33x$	16.8***	36	71
Melampyrum nemorosum	79	$-1.27+1.67x$	12.6***	48	121
Gentianella germanica	66	$-1.54+1.30x$	7.9**	53	749
Rhinanthus serotinus	81	$-1.28+1.52x$	6.8**	48	197
		$-1.90+1.61x-2.2y$	12.6**		
Gentianella ciliata	65	$-0.99+1.29x$	5.8*	54	291
Melampyrum arvense	73	$-0.57+0.89x$	4.5*	48	1276
Thlaspi perfoliatum	77	$-0.31+1.05x$	3.9*	34	245
Rhinanthus minor	84	$0.14+0.81x$	1.1 ns	38	

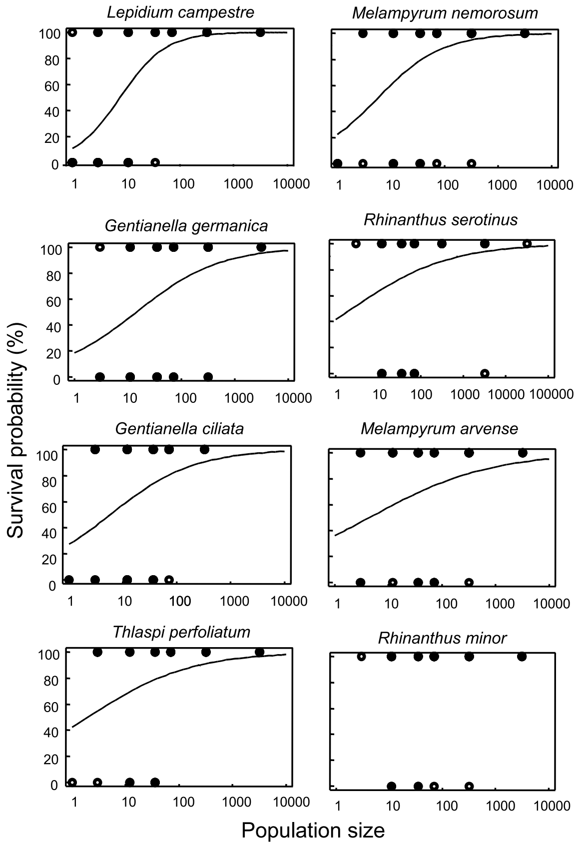

Fig. 2. The relationship between size of a population in 1986 and its probability of survival until 1996 for eight endangered plant species in southern Lower Saxony, Germany. Time between surveys had no significant effect ($p < 0.05$ for all species). Logistic regression curves are shown if significant. Open circles denote single populations, filled circles several populations of the same size class.

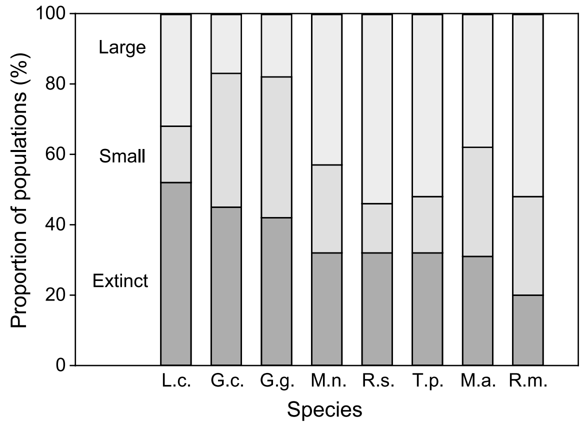

Fig. 3. The proportion of small populations (<100 individuals in 1986) of eight threatened plants that became extinct, stayed small or developed into large populations (>100 individuals) from 1986–1996. L.c., *Lepidium campestre;* G.c., *Gentianella ciliata*; G.g., *Gentianella germanica*; M.n., *Melampyrum nemorosum*; R.s., *Rhinanthus serotinus*, T.p., *Thlaspi perfoliatum*; M.a., *Melampyrum arvense*; R.m., *Rhinanthus minor*.

tion among species in the number of plants necessary in a population to make its survival likely. The population size necessary for 90% probability of survival over 10 years varied from 71 individuals for *L. campestre* to 1276 for *M. arvense* (Table 1). In *R. serotinus* survival probability of a population not only increased with its size, but also with decreasing distance to the nearest population. In all other species distance had no effect.

Not all small populations were doomed to extinction. While many of the small populations with less than 100 individuals became extinct, a considerable proportion survived in all species as small populations and some even developed into large populations (>100 individuals, Fig. 3). This was true even for the very small populations (<26 plants).

The mean annual growth rate (λ) of the surviving populations during the study period differed strongly among the eight species ($F_{7,252} = 5.7$, $p < 0.001$). In four of the species (*G. ciliata*, *M. arvense*, *M. nemorosum* and *T. perfoliatum*), the mean annual growth rate of populations (λ) was not significantly different from 1 (t-test, $p > 0.05$), i.e. their size in 1996 was about the same as in 1986 (Fig. 4). In three species (*L. campestre*, *R. minor* and *R. serotinus*), mean population size increased significantly ($\lambda > 1$, $p < 0.05$) and only in *G. germanica* did the mean size of the surviving populations decrease ($\lambda = 0.43$, $p < 0.05$) during the study period.

Discussion

In seven of the eight studied plant species the probability of survival increased significantly with population size. In *R. minor* the overall risk of extinction was relatively low and the relationship between survival and popula-

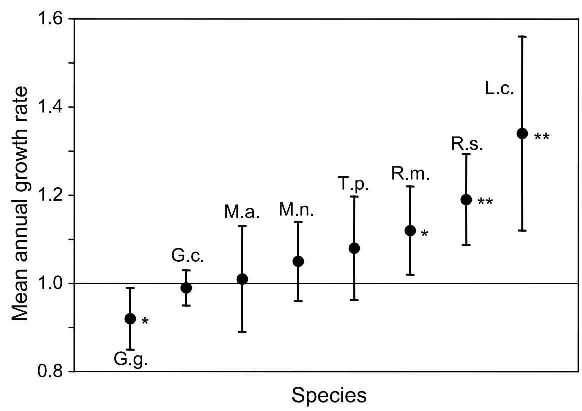

Fig. 4. Mean annual growth rate of surviving populations of eight threatened plants from 1986 to 1996. Vertical bars denote the 95% confidence intervals. Asterisks indicate growth rates significantly different from 1. *, $p < 0.05$; **, $p < 0.01$. For explanation of species abbreviations see Fig. 3.

tion size was not significant, but the regression coefficient had the expected sign. Thus, our results provide empirical evidence for the suggested important role of small population size for the extinction of local plant populations (Menges 1991a, 1998). Similar observations have been made in studies that have investigated the relationship between population size and survival in animals, e.g. in birds (Pimm et al. 1988, Bellamy et al. 1996), bighorn sheep (Berger 1990), small mammals (Lima et al. 1996) and butterflies (Thomas 1994a, Nieminen 1996, Krauss et al. 2003). Two previous studies on plants, which were, however, not based on actual numbers of plants, but used substitutes like species area (Ouborg 1993) or cover (Fischer and Stöcklin 1997) for population size, have also reported negative effects of small population size on survival. In contrast, Husband and Barrett (1996) found no such relationship in *Eichhornia paniculata,* an aquatic plant of ephemeral pools in north-east Brazil, which they attributed to the frequent catastrophic changes in local environmental conditions that result in the extinction of populations regardless of their demographic characteristics.

There are several possible explanations for the observed relationship. First, there could have been a general deterministic decline in population sizes in the study area due to habitat deterioration. For a given decline, small populations are likely to become sooner extinct than large ones (Thomas 1994b). However, only in one species (*G. germanica*) a significant decline in mean population size of surviving populations was observed over the study period. Our estimate of the mean growth rate was based on the growth rate of populations that survived. Because populations with low growth rates will go extinct more often than those with a high growth rate, the mean growth rate of all populations was probably somewhat lower. However, even including populations that became extinct, overall more than 40% of all populations had stable population sizes or increased in size. Thus, a general deterministic decline in the number of individuals is unlikely as an explanation for the observed relationship between population size and extinction.

Second, although no general decline in population sizes was found, the higher extinction rate of small populations could be due to a deterministic decline of the number of individuals in small populations. Populations that were small in 1986 might have been small because they occurred in habitats where conditions had deteriorated and thus might have been on their way to deterministic extinction. Negative changes in habitat quality cannot be excluded and may well have contributed to the observed local extinctions. However, in all species a considerable proportion of the small populations survived and even developed into large populations, indicating that habitat quality was not always worse in small than in large populations. This suggests that stochastic processes were at least partly responsible for the increased extinction risk of small populations. Environmental stochasticity is the most likely cause, but genetic stochasticity might have contributed, e.g. in the case of *Gentianella germanica* (Fischer and Matthies 1998a, b). Simulation studies suggest that even moderate fluctuations of environmental quality greatly increase the extinction risk for small populations (Menges 1998).

In contrast to earlier studies involving plants, in the present study the precise location and the number of individuals was known for each population. This made it possible to analyse empirically the relationship between the number of individuals in a plant population and its survival probability and to estimate the number of plants necessary for a certain probability of survival ("minimum viable population size", MVP, e.g. Menges 2000). These empirical estimates have the advantage that they are based on observations of real extinction events in a large number of populations over a comparatively long period of time, whereas most simulation studies of extinction risks for plants are based on few populations and demographic data from less than five years (Menges 2000). In contrast, simulation models have the advantage that they are far more versatile, can be used to study different scenarios (e.g. effects of managements) and cover different periods of time.

The quantitative estimates of MVPs must, however, be viewed with caution, because due to the log-scale for population size small changes in the relationship will result in large changes in the estimated MVP (Fig. 2). Overall, the results show that very small populations of the studied short-lived plants faced a considerable risk of extinction even over a period of only ten years, while the risk for populations with >1000 individuals was very small.

Judged by their MVPs (71–1276 individuals for 90% probability of survival over ten years) there was considerable variation among the studied species in the number of plants necessary to make survival of a population likely. These differences are not easily explained by life-history traits of the plants. Traits that are known to affect the risk of extinction include longevity and the size and persistence of the seed bank (Pimm et al. 1988, Stöcklin and Fischer 1999). The studied species are all short-lived and most have transient seed banks (*Melampyrum*: Matthies 1991, *Rhinanthus*: Ter Borg 1985, *G. ciliata*, Thompson et al. 1997) or seed banks that are short-term persistent but depleted quickly (*L. campestre*, Roberts and Boddrell 1983). Of the two species with a more persistent seed bank (Baskin and Baskin 1979, Fischer and Matthies 1998c), *G. germanica* had a much larger MVP than had *T. perfoliatum.* Moreover, closely related pairs of species with the same life-history like *Melampyrum arvense* and *M. nemorosum* and *Rhinanthus serotinus* and *R. minor*, differed strongly. This suggests that differences in maximum population growth rates (Fagan et al. 2001), about which little is known for plants, or individual combinations of traits may be responsible for the differences in the number of plants necessary to make population survival likely.

Based on simulation models the number of plants necessary to ensure a risk of extinction of less than 5% over 100 years has recently been estimated as 170 plants for the long-lived forest perennial *Panax quinquefolium* (Nantel et al. 1996) and as 25 genets for the clonal perennial woodland herb *Asarum canadense* (Damman and Cain 1998). The risk of extinction increases with the length of the time period considered and the required survival probability and these estimates of MVPs are therefore not directly comparable to the values obtained in the current study. However, although we considered a much shorter period of time and allowed a higher risk, most of our estimates of MVPs were much higher than the quoted numbers, suggesting that the studied species are far more sensitive to small population size than *Panax* and *Asarum*. These differences are consistent with the expectation that short-lived plants are more sensitive to environmental stochasticity than long-lived plants (Pimm et al. 1988, Quintana-Ascencio and Menges 1996), at least in the absence of a persistent seed bank.

The persistence of populations could in principle reflect re-colonisations rather than real persistence. If re-colonisations were frequent one would expect populations that were close to another population to have a lower probability of extinction. However, only in *R. serotinus* was survival related to the distance to the nearest conspecific population. Moreover, none of the studied species has special adaptations to the long range dispersal of seeds and for most of them it is known that dispersal is very limited, e.g. for *Melampyrum* spp. (Matthies 1991), *L. campestre* (Thiede and Augspurger 1996), *G. germanica* (During et al. 1985, Fischer and Matthies 1998a, b) and *Rhinanthus* spp. (Ter Borg 1985). Moreover, very few new populations have been found in Lower Saxony despite the long-time assessment programme and, even in those cases, it cannot be excluded that they had only been overlooked earlier (E. Garve, pers. comm.). Thus, the studied plants belong to the many species for which in the current fragmented landscape metapopulations do not occur at a steady state because there is less colonisation than extinction (Hanski et al. 1996).

In conclusion, our results provide empirical evidence for the predicted negative relationship between size and probability of extinction of local plant populations and stress the importance of stochastic factors for extinction. However, the results also suggest that the number of individuals required to make population survival likely may vary strongly even among closely related species (Franklin 1980). Small populations of rare species have sometimes been considered to have negligible conservation value (Lesica and Allendorf 1992, Lamont et al. 1993), because it has been suggested that below a certain threshold size local populations will enter an extinction vortex, i.e. a spiral of ever decreasing population size (Gilpin and Soulé 1986, Lamont et al. 1993). However, there may be some hope even for quite small plant populations, as exemplified by the fact that in all studied species some very small populations survived and developed into large populations, suggesting that extinction is not inevitable.

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