# AN ABSTRACT OF THE THESIS OF

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Title: Biosystematic Studies of the Mimulus Moschatus
Complex in the Pacific Northwest

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Populations of an unknown species of Mimulus, herein
described as Mimulus hymenophyllus Meinke, were located
and studied near Horse Creek, a tributary of the Snake
River in eastern Wallowa County, Oregon. The new species
is differentiated from its apparent closest relative,
Mimulus jungermannioides Suksd., by an annual habit, long
petioles, corollas that are three to four times the length
of the calyx, rounded capsules, and seeds up to 0.85 mm
long. Mimulus hymenophyllus and M. jungermannioides are
members of the section Paradanthus, and are
morphologically allied with Mimulus moschatus Dougl. in
Lindl. and several related taxa. The Mimulus moschatus
complex of species is distinguished within the genus by
having firmly adherent placentae, glandular-sticky foliage
and stems, prismatic calyces with equal to sub-equal
teeth, elongate pedicels, and deciduous, funnelform
corollas ranging in color from canary to lemon yellow.

Mimulus hymenophyllus is endemic to the steep canyons of Horse and Cow Creeks in Wallowa County, at altitudes ranging from 850 to 1300 m. The species is restricted to the damp crevices of vertical basalt cliffs, often growing in the shade under overhangs. The surrounding plant community is dominated by several coniferous species, primarily Pseudotsuga menziesii, Pinus ponderosa, and Abies grandis. The habitat of M. hymenophyllus is isolated, and is presently not in danger from human disturbance. However, the species is currently maintained as a state and federal candidate for listing as threatened or endangered, based on limited abundance and narrow geographic range.

Studies of the seed and seedling biology of Mimulus hymenophyllus and its Pacific Northwest relatives (i.e., M. moschatus, M. floribundus, M. jungermannioides, M. patulus, M. pulsiferae, M. washingtonensis, and M. breviflorus) were also conducted. Germination trials indicated that seeds of M. moschatus, M. jungermannioides, and M. floribundus are capable of germination immediately or soon after capsules dehisce, and do not become dormant upon later exposure to warm or cold temperatures. Seed lots of M. hymenophyllus and M. breviflorus germinate rapidly when first mature, but subsequently develop complete or partial dormancy after prolonged exposure to late summer temperatures. Dormant seeds of these species, as well as those of M. patulus, M. pulsiferae, and M.

<u>washingtonensis</u> which are dormant when capsules dehisce, will germinate readily after several weeks of cold-wet stratification.

Four of the five species lacking innate seed dormancy develop inflated fruiting calyces that temporarily trap seeds as capsules dehisce. This prolongs the dispersal rate of seed crops, thereby minimizing the potential for catastrophic seedling mortality due to mass germination of cohorts during unfavorable environmental conditions. These species retain seed on the parent plant for significantly longer periods than species with unmodified calyces. Seed dispersal from parent plants is accomplished by wind and flowing water, except in <u>M</u>. <u>hymenophyllus</u>, where negatively phototropic pedicels orient ripe capsules towards the darkened cliff substrate for dispersal directly into crevices.

Two of the rarest species studied, <u>M</u>. <u>hymenophyllus</u> and <u>M</u>. <u>patulus</u>, were found to co-occur in nature with an indigenous and rather weedy, unrelated species of <u>Mimulus</u>, i.e., <u>M</u>. <u>nasutus</u> Greene. Experimental plantings showed that seedling lots of <u>M</u>. <u>nasutus</u> emerge sooner and over a shorter period than those of the two uncommon species, suggesting that <u>M</u>. <u>nasutus</u> may outcompete them and thereby contribute to their rarity.

Seedlings of <u>M</u>. <u>breviflorus</u> and <u>M</u>. <u>floribundus</u>, which typically occur in habitats subject to sudden fluctuations in soil moisture, exhibit adaptations for accelerated

sexual reproduction under experimental drought conditions. This trait, when coupled with inflated fruiting calyces, enables these species to exploit unpredictably arid environments despite the potential disadvantage of nondormant seeds. Mimulus jungermannioides and M. moschatus are not adapted for precocious sexual maturation, and offset their lack of seed dormancy by having a perennial life cycle and by occurring in more predictably mesic habitats. Significant differences between the annual and perennial species were observed in the timing and amount of seed production during drought-stress.

The information provided in this thesis will be valuable to systematists and conservation biologists. Several of the species studied have been promoted for protection under endangered species laws. The formal naming of Mimulus hymenophyllus legitimizes efforts for the management of this unique species, while seed and seedling biology data will be important to germplasm studies, phylogenetic assessments, and possible re-introduction of species or populations should extirpation occur.

Biosystematic Studies of the <u>Mimulus</u> <u>moschatus</u>
Complex in the Pacific Northwest

by

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Typed by Robert James Meinke for _____Robert James Meinke_

This thesis is dedicated to

**Brennan** and **Tristan**

## ACKNOWLEDGEMENTS

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## CHAPTER I:

## INTRODUCTION AND OVERVIEW

The monkeyflower genus Mimulus L. (Scrophulariaceae), comprised of small to medium-sized annual and perennial herbs, was initially described by Linnaeus (1741) from collections of Mimulus ringens gathered in coastal Virginia during the early eighteenth century. Over the next several decades, the genus was shown to have a virtual world-wide distribution, with species eventually being discovered on every continent except Europe and Antarctica (Grant 1924). In the only monographic treatment of Mimulus, Grant (1924) recognizes 114 extant species, 35 varieties, two naturally occurring hybrids, one fossil species, and nine "doubtful and little-known species." Modern North American floristic accounts of the genus vary considerably in the number of taxa accepted. Cronquist (1959) and Holmgren (1984) estimate approximately 100 known species of Mimulus, while Pennell (1951) and Munz (1959) place the total at nearly 150. These discrepancies are largely based on differing interpretations of several morphologically complex species groups.

Mimulus is geographically centered along the west coast of the United States, in the Californian and Sierran Biotic Provinces delineated by Munz (1959). Of the 114 species circumscribed by Grant (1924), 74 occur in California, with 51 of these endemic to that state. Many of these species are among the most visibly impressive of the spring wildflowers of the Pacific coast, commonly occurring in dense, showy stands.

Secondary regions of taxonomic diversity in Mimulus occur in Oregon east of the Cascade Mountains, and in central montane Chile (Grant 1924, Vickery 1978). Scattered occurrences of individual taxa and minor species complexes extend the range of Mimulus to eastern North America, Japan, southern China, India, Nepal, New Zealand, Australia, Madagascar, and southern Africa. The relationships of many of these isolated taxa are obscure, suggesting that the genus is one of the oldest in the family Scrophulariaceae (Grant 1924).

The high concentration of species in California has led to speculation that Mimulus evolved there, and that the widely disjunct taxa have arisen later as a result of isolation following long distance dispersal (Pennell 1920, Grant 1924, Vickery 1978). All of the species with non-North American distributions occur primarily in perennially wet habitats, such as marshes or riverbanks. This is consistent with Pennell's (1920) theory of seed

dispersal by migratory waterfowl. Moreover, a number of widespread western North American species of Mimulus may also be distributed by aquatic birds, implied by fragmented distributions correlated with vernal pools and streams. Such species are located primarily in cismontane California and the Great Basin, and in the dry interior valleys of southwest Oregon (Munz 1959, Peck 1961, Holmgren 1984).

Although monkeyflower species are not all constrained to grow in wet habitats throughout their life cycle, most require at least the continuous imbibition of over-wintering seeds for germination to occur, as well as persistently moist conditions for a period thereafter to ensure recruitment (Ezell 1971; Meinke, unpublished). The macrohabitats of North American species of Mimulus range from sub-tropical to arctic-alpine. However, most North American species occur within temperate zones at low to middle elevations, including a high number of regional endemics adapted to deserts or areas with seasonally arid climates (Grant 1924, Holmgren 1984). Ecological specialization in the genus is particularly evident in these drier areas, where localized species are restricted to sand dunes, vertical rock outcrops, arroyos, alkaline depressions, or serpentine barrens (Cronquist 1959, Munz 1959, Holmgren 1984).

Mimulus is characterized, at the species level, by a
wide array of life history strategies. Although most, and
possibly all, species are genetically self-compatible
(Grant 1924, Clausen and Hiesey 1958, Hiesey et al. 1971,
Vickery 1978; Meinke, unpublished), there is considerable
between-species variation in morphological features
associated with reproduction. Mimulus flowers are often
conspicuously bilabiate, with corollas that are
predominantly red, yellow, blue, or a combination of these
colors (Grant 1924). The few studies that have focused on
the pollination biology of Mimulus report a diverse suite
of floral visitors to the showier species, including
hummingbirds, flies, bees, and butterflies (Hiesey et al.
1971, Kiang 1973, Vickery 1978, Harris 1979). Self-
pollination in the genus is also occasionally observed.
However, strict autogamy is primarily manifested in
drought-tolerant races or ecotypes of otherwise
facultative outcrossers, such as M. guttatus, as there are
very few species of Mimulus that are obligately self-
pollinating. Species of Mimulus possessing facultative,
or mixed, breeding systems have been demonstrated to have
highly variable selfing rates (Ritland and Ganders 1987)
and significant reproductive plasticity within and among
populations (Douglas 1981, Waser et al. 1982). All
species are capable of maturing from several dozen to
several hundred seeds per fruit and numerous fruits per

plant, and most produce copious amounts of pollen. Despite the large numbers of ovules in each ovary the pollen/ovule ratios (Cruden 1977) of most species are comparatively high and suggest adaptation for outcrossing (Meinke, unpublished).

## THE MIMULUS MOSCHATUS COMPLEX

Mimulus is comprised of numerous groups of phylo-genetically and taxonomically allied species based on morphologic and cytologic evidence (Grant 1924, Vickery 1978). Some of the larger species complexes are quite diverse and several of these incorporate, individually, much of the range of general ecological and reproductive variation known from the genus as a whole. One such complex is centered around the common musk monkeyflower, Mimulus moschatus Dougl. in Lindl., a creeping perennial indigenous to forest and steppe from British Columbia to southern California, and naturalized in Europe (Grant 1924, Munz 1959, Peck 1961). Species in the Mimulus moschatus complex may be annual or perennial, and are differentiated within the genus by their firmly adherent placentae (not separating at maturity), glandular-viscid pubescence on the leaves and stems, long pedicels, prismatic calyces with equal to subequal teeth, and funnelform, deciduous corollas ranging from canary to lemon yellow. This group has been placed by Grant (1924)

in the section _Paradanthus_, a taxon considered by
contemporary systematists to represent a polyphyletic
assemblage (Vickery 1978, Argue 1980) devised to
accommodate species "which (do) not seem to belong to any
of the well-established (lineages)" in _Mimulus_ (Grant
1924).

The only frequently encountered species in the
complex, other than _Mimulus moschatus_, is _M. floribundus_
Dougl. in Lindl., a morphologically and ecologically
diverse annual native to every state west of the Great
Plains, with disjunct populations in Arkansas and Jalisco,
Mexico.  The remaining members of the group are narrow
endemics, or occur very sporadically over geographic
ranges that include one to three states (Grant 1924,
Cronquist 1959, Munz 1959, Holmgren 1984).  The local
endemics in the _M. moschatus_ complex occur in two distinct
regions.  One cluster of species is found primarily on
granitic substrates on the mesic west slope of the
southern Sierra Nevada, and includes _Mimulus arenarius_
Grant, _M. dudleyi_ Grant, _M. norrisii_ Heckard and Shevock,
and _M. floribundus_ var. _subulatus_ Grant.  Species
comprising the other group are apparently basalt
obligates, with populations situated in the arid canyons
and valleys of northeast Oregon and adjacent areas - these
are _Mimulus jungermannioides_ Suksd., _M. washingtonensis_
Gand., _M. ampliatus_ Grant, and _M. patulus_ Penn.

The two groups of narrow endemics are completely allopatric, separated at their closest point by an 800 km expanse of the northern Great Basin. Spanning this distribution gap are <u>Mimulus</u> <u>breviflorus</u> Piper and <u>M</u>. <u>pulsiferae</u> Gray, diminutive species that are widespread but scattered and frequently overlooked. Both of these taxa have been collected from a wide range of soil types, including basaltic- and granitic-based substrates.

## STUDY OBJECTIVES

In this thesis, attention is focused on those species of the <u>Mimulus</u> <u>moschatus</u> complex native to the Pacific Northwest. Several of these have been evaluated in recent years with regard to their suitability for listing as threatened or endangered species, as defined by the federal Endangered Species Act, various state statutes, government agency regulations, and private interest groups (Siddall et al. 1979, Sheehan and Schuller 1981, The Nature Conservancy 1989). Past recommendations concerning the legal status, conservation, and management of these rare species have been based almost entirely on distributional and anecdotal accounts. Although state and federal governments are required, by law, to gather more substantial evidence before listing a plant species as threatened or endangered, there have been no taxonomic or biologically-oriented studies of this group of endemics.

The data presented herein are expected to contribute to the prerequisite information base necessary for the listing of taxa under endangered species statutes.

Following this general Introduction, the second chapter of the thesis (pages 10-19) is comprised of a new species description for a distinctive series of *Mimulus* populations recently found near the Snake River in eastern Wallowa County, Oregon. This taxon was initially identified as a disjunct occurrence of the rare *Mimulus jungermannioides* of north-central Oregon, and is considered morphologically aligned with the *M. moschatus* complex. The third chapter (pages 20-51) reports on the seed dispersal, germination requirements, and seedling emergence ecology of the *M. moschatus* complex in the Pacific Northwest, including the new species from Wallowa County. Conclusions and final comments are presented in Chapter IV (pages 52-56).

Taxonomic and ecologic studies of *Mimulus moschatus* and its relatives have pragmatic as well as academic applications. State and federal laws generally stipulate that any plant population threatened with extinction must first be taxonomically recognized and described in the literature before being listed as threatened or endangered, or considered for special management and protection. Thus, the description of the new species will have applied value to those agencies managing its habitat.

In addition, the data gathered on seed biology, particularly for the rare and local taxa, will have practical uses should programs for the propagation, seed banking, recovery, and re-establishment of extinct populations or species be implemented.

This information will also be useful in future monographic and evolutionary studies of _Mimulus_. Although rarely available, information detailing the biological distinctions between related species can be extremely useful in the evaluation of phylogeny and the construction of meaningful classifications. Finally, the apparent variation represented in the study group selected here will allow for comparisons between seed characteristics and life cycle (annual versus perennial), breeding system (facultative versus obligate inbreeder), level of rarity (widespread versus narrow endemic), and habitat (rock wall versus alluvium). There have been few generic level studies where a closely related but reproductively diverse group of species has been examined collectively in terms of life history traits.

CHAPTER II:

<u>MIMULUS</u> <u>HYMENOPHYLLUS</u> (SCROPHULARIACEAE), A NEW SPECIES

FROM THE SNAKE RIVER CANYON AREA OF EASTERN OREGON

INTRODUCTION

Extreme northeastern Oregon is one of the botanically
least explored areas of the western United States. Of
particular interest within this region is the rugged
corridor of ridges and canyons immediately west of the
Snake River in Wallowa County, paralleling the Idaho
border from the Wallowa Mountains north to the Washington
state line. During a recent collecting trip here an
undescribed, annual to short-lived perennial species of
<u>Mimulus</u> was discovered growing under diffuse sunlight in
the moist cracks of deteriorating basalt cliffs. This
fragile monkeyflower is the only member of its genus whose
known geographic range is confined to Oregon, although it
would not seem unreasonable to expect that future field
work may uncover it in similar habitat in adjacent Idaho
as well.

DESCRIPTION

**Mimulus hymenophyllus** Meinke, species novum (Fig. 1).
Herbae annuae aut perennes, pubescentes, viscido-
villosae; caulibus infirmis, 0.5-2.5 dm longis,
suberectis, ramis paucis, internodis longis; foliis

**Figure 1.** Adult plants of <u>Mimulus</u> <u>hymenophyllus</u> Meinke, growing on a vertical basalt cliff along Horse Creek, within the Snake River drainage of eastern Wallowa County, Oregon. This photograph was taken at the type locality for the species, located in a <u>Pinus</u> <u>ponderosa</u> - <u>Pseudotsuga</u> <u>menziesii</u> - <u>Abies</u> <u>grandis</u> forest that parallels the riparian zone of Horse Creek.

caulium paucis, oppositis, tenuibus, late lanceolatis vel
ovatis, denticulatis, 1.0-3.5 cm longis, petiolo lamina
plerumque longiore, divaricato; pedicellis axillaribus,
tenuibus, reflexis aut ascendentibus; calyce in statu
florifero (2.5)-3.5-5.5(-6.0) mm longo, in statu
fructifero late campanulato, infirme angulato, 4.0-7.0 mm
longo, dentibus cilatus, 0.5-1.2 mm longis, aequalibus,
late triangularibus, acutis; corolla flava, infundibulari,
(15-)18-28 mm longa, calyce 3-4 plo longiore, tubo
angusto, exserto, labiis plus minusve inaequalibus,
patulis; staminibus stylo brevioribus, inclusis, glabris;
stylo fere glabro, incluso, labiis stigmatis aequalibus;
capsula inclusa, subglobosa; seminibus (0.5-)0.65-0.85 mm
longis, late oblongis, longitudinaliter rugatis.

Delicate annual to rarely short-lived perennial herb,
typically growing in masses, prostrate to suberect,
sparsely glandular-villous with slimy to viscid
transparent hairs less than 0.8 mm long; stems few to
several, fragile and thin, 0.5-2.5 dm long, winged,
arising from numerous reddish-orange capillary roots or
occasionally rhizomes, sparingly branched throughout, with
long internodes; leaves few, cauline and basal, generally
three to seven opposite pairs per primary stem; leaf
blades thin, filmy, broadly lanceolate to ovate, acute,
subpalmately veined, 1.0-3.5 cm long and equally wide or
slightly less, shallowly denticulate to nearly entire,

broadly triangular at the base and tapering or
occasionally cordate; petioles of cauline leaves equal to
or usually exceeding the leaf blades, generally less than
the internodes, diverging, prominently winged; flowers in
axillary pairs; pedicels narrower than the petioles,
slightly winged at the base, reflexed or usually
ascending, ranging from 0.5-1.8 times the petiole length
but seldom exceeding the blades; calyx green, the tube
narrowly triangular and evidently angled, acute at the
base or slightly rounded, with scattered glands on the
angles, calyx in its entirety (2.5-)3.5-5.5(-6.0) mm long
at anthesis, moderately inflated in fruit, becoming
campanulate but not lengthening significantly, up to 7.0
mm long and nearly as wide; calyx teeth equal, 0.6-1.2 mm
long, about half again as broad, deltoid and abruptly
acute in flower, rounded and mucronate in late fruit, with
simple acerose eglandular cilia on the margins; corolla
funnelform, weakly bilabiate with an open orifice, (15-)
18-28 mm long (3-4 times the length of the calyx), light
yellow with scattered red or purplish dots on the throat
and lower lobes, puberulent externally with a tuft of
thickened yellow hairs on the inner lower lip, the tube
half again as long as the calyx, the throat moderately
flaring, the lobes short and spreading, typically entire
or apically notched; stamens glabrous, included, 1/2-3/4
the length of the corolla; style glabrous or with a few

hairs, included, exceeding the stamens; stigma lips more or less equal and rounded to lanceolate, glabrous or fringed; capsule essentially glabrous, oval to rounded, the tip abruptly apiculate to shallowly retuse, barely included in the calyx tube at maturity, 3.0-6.0 mm long and 2.5-5.7 mm wide, short stipitate, the placentae firmly adherent through the apex; seeds ovoid to oblong, blunt, longitudinally wrinkled, (0.5-)0.65-0.85 mm long, 25-70 (-95) per capsule; pollen grains large, tricolporate with semitectate, microreticulate exines, diameter (mean, followed parenthetically by range) of polar axis 41.4 (34.0-46.1) microns, equatorial axis 44.4 (37.5-49) microns.

Type Collection.--USA, Oregon, Wallowa County, loosely erect or hanging from seasonally moist basalt cliffs with southwestern exposures, mostly in partial shade or occasionally full sunlight, on the east side of Horse Creek, ca. 12 km south of the Imnaha River and ca. 21 km west of the Snake River (Township 1 North, Range 49 East, Section 7), 1075 m, 2 July 1980, Meinke & Kennison 2656 (Holotype: OSC; isotypes: ID, NY, ORE, UC, US, WS, WTU).

Paratypes.--USA, Oregon, Wallowa County: (1) along Horse Creek (Township 2 North, Range 48 East, Section 36), 900 m, 20 June 1979, Leary and Leary 3312 (OSC); (2) Horse

Creek, ca. 14 km south of the Imnaha River, 1150 m, 26 June 1979, Meinke, Leary, and Bafus 2365 (OSC).

Habitat.--Mimulus hymenophyllus is restricted, insofar as is currently known, to the deep canyons of Horse and Cow Creeks in southeast Wallowa County, Oregon at altitudes ranging from 850 to 1300 m. Populations of the species are scattered on steep cliffs of gray basalt with western or southwestern aspects, occurring within narrow, isolated bands of Pseudotsuga menziesii-Pinus ponderosa forest maintained by the northerly downward flow of cool air from the upper slopes of the Wallowa Mountains. Additional species occurring with M. hymenophyllus include Holodiscus discolor, Symphoricarpos albus, Berberis repens, Ribes velutinum, R. aureum, Penstemon wilcoxii, P. triphyllus, Glossopetalon nevadensis var. stipuliferum, and Cystopteris fragilis. There are several other drainages in the area with physiognomy similar to Horse Creek canyon which, although unexplored, are anticipated to shelter populations of M. hymenophyllus as well.

Flowering in the new species is initiated in late April and may continue more or less unabated through August or early September, depending on elevation and available moisture. Capsules first mature in late May or early June.

# TAXONOMIC RELATIONSHIPS

Mimulus hymenophyllus apparently is most closely
related to M. jungermannioides Suskd. (section
Paradanthus), a localized perennial endemic to basalt
outcrops in the Columbia River Basin of north-central
Oregon and reputedly adjacent Washington (Pennell 1951,
Cronquist 1959). The two species possess lax habits of
similar form and size, both being adapted to damp crevices
in steep, basalt cliffs overlooking riparian zones. In
addition, their pubescence type, shape and venation of the
leaf blades, and calyx construction are essentially
identical. There are a number of clearly marked
morphological and ecological differences between the taxa,
however, amply justifying separation at the species level.
These distinctions are specified in Table 1.

The known populations of M. hymenophyllus and M.
jungermannioides are widely separated geographically.
Their respective narrow distribution patterns suggest that
they may be glacial relicts, but their evolutionary
relationship to each other and related elements within the
section Paradanthus have yet to be assessed. The
relatively scant seed production, large seed size, and
exceptional pollen grains of M. hymenophyllus, the latter
feature the largest reported for the section (Argue,
unpublished data), are reminiscent of a polyploid
condition (Argue, personal communication; Stebbins 1971).

Table 1. Morphological and ecological distinctions between <u>Mimulus</u> <u>hymenophyllus</u> Meinke and <u>M</u>. <u>jungermannioides</u> Suksd.

| Character | <u>M</u>. <u>hymenophyllus</u> | <u>M</u>. <u>jungermannioides</u> |
|---|---|---|
| <u>Morphology</u> | | |
| Reproduces vegetatively | No | Yes |
| Leaves | Petioles exceeding blades | Petioles less than blades |
| Pubescence | Sparse, hairs all less than 0.8 mm long | Moderate to very heavy, many hairs 1.0-1.5 mm long |
| Fruiting pedicels | 0.5-1.8 times petiole length | (2.5-)4-15 times petiole length |
| Calyx length | 3.5-5.5 mm in flower | 5.0-9.0 mm in flower; up to 12.5 mm in fruit |
| Corolla length | 18-28 mm, 3-4 times calyx length | 14-20(-24) mm, 1.8-3 times calyx length |
| Capsule | 3.0-6.0 mm long, rounded to ovate, mucronate | 5.0-9.0 mm long, eliptic to lanceolate |
| Seeds | 0.65-0.85 mm long, 25-70(-95) per capsule | 0.35-0.5 mm long, 75-200 per capsule |
| Pollen grain diameter (mean): | | |
| Polar axis | 41.4 $\mu$ | 31.0 $\mu$ |
| Equatorial axis | 44.4 $\mu$ | 34.4 $\mu$ |
| <u>Ecology</u> | | |
| General habitat | Within mesic coniferous forest | Within xeric sagebrush-bunchgrass |
| Elevational range | Ca. 850-1300 m | Ca. 95-370 m |

Chromosome counts, however, remain to be completed for both species.

In her monograph of the genus _Mimulus_, Grant (1924) allied _M. jungermannioides_ with _M. moschatus_ Dougl. in Lindl. and _M. floribundus_ Doug. in Lindl., two polymorphic species widespread in western North America, and _M. arenarius_ Grant, a regional endemic of the south-central Sierra Nevada in California. _Mimulus hymenophyllus_ also displays strong morphological affinities to this assemblage, with all of the species sharing a similar symmetrical calyx structure and an unusual sticky to slimy glandular vesture on the vegetative parts. The adaptive significance of this exudate, which varies in intensity from species to species, has not been determined. Recent pollen analysis of the genus (Argue 1980, and unpublished data) tends to corroborate this proposed taxonomic alliance. Palynological studies also indicate, in support of Pennell (1951), that a reevaluation of the broad species concept which is generally accepted today for _M. moschatus_ might be appropriate. Pennell advocates taxonomic recognition of several morphogeographic phases of _M. moschatus_, in spite of relatively broad zones of intergradation. A revival of this interpretation founded on current evidence would probably have implications in future evolutionary studies of _M. hymenophyllus_ and its relatives. It is suspected that _M. hymenophyllus_ and

M. jungermannioides are common derivatives of one of these forms of M. moschatus, possibly splitting from that entity as a single unit and then diverging later under local ecological pressure.

Mimulus hymenophyllus is noteworthy in that it is the single member of its large genus that may be endemic to Oregon. Although it has been recorded from only a few small populations, it exists in remote country far from significant disturbing influences. Development of this area in the foreseeable future by government or private interests appears very unlikely. Therefore, despite its overall rarity and limited occurrence within its range, this species should not be considered actively threatened or endangered at this time. Periodic monitoring of M. hymenophyllus will be important, however, and the species should be maintained on the list of taxa considered to be official candidates for protection under federal and state conservation regulations.

CHAPTER III:

COMPARATIVE STUDIES OF SEED GERMINATION AND DISPERSAL

ECOLOGY IN THE

<u>MIMULUS</u> <u>MOSCHATUS</u> COMPLEX (SCROPHULARIACEAE)

INTRODUCTION

The persistence of an annual or herbaceous perennial plant in a particular habitat requires that all stages of its life cycle be adapted for specific environmental parameters (Baskin and Baskin 1971, Harper 1977, Grime 1979). Especially critical are the rate and timing of seed germination and seedling establishment. The time at which a seed germinates relative to the external environment and the growth of potential competitors is a determinant of its success as an organism (Silvertown 1982). In plants possessing seeds capable of germinating at high percentages when first mature, germination and growth typically proceed under benign, predictable conditions. A lack of germinability following dispersal suggests that seeds are adapted to respond to cues signaling favorable environments. Germination delays may be related to physiology or impermeable seed coats (innate dormancy), or to external, often climate-controlled factors (induced and enforced dormancy) (Harper 1957, 1977). Genetically- or environmentally-controlled delays of germination are considered adaptations for seedling

survival in given habitats (Vegis 1964, Baskin and Baskin 1971, Angevine and Chabot 1979, Silvertown 1982, 1984, Willson 1984).

In species restricted to narrowly defined habitats, selection may act rapidly in establishing advantageous germination phenologies. Variation in germination strategies within closely related groups of taxa occurring in similar habitats may be indicative of such selective pressure. While considerable research has been conducted on the germination behavior of individual species (see reviews by Harper 1957, Wareing 1966, Roberts 1972, Mayer and Poljakoff-Mayber 1975, Silvertown 1984) and of taxonomically unrelated groups from common selective regimes (e.g., Ratcliffe 1961, Pemadasa and Lovell 1975, Young and Evans 1975, van der Valk and Davis 1976, Baskin and Baskin 1977, Grime et al. 1981), studies focussing on the germination strategies present within evolutionally allied species groups are less frequent (see Beadle 1952, Harper 1957, Baskin and Baskin 1971, Keeley and Tufenkian 1984).

This paper contrasts the seed germination and dispersal characteristics of the _Mimulus_ _moschatus_ complex in the Pacific Northwest (taxonomy after Grant 1924, Pennell 1951). Except for research by Vickery (1963, 1967, 1983) and Ezell (1971), little information is available concerning germination patterns in _Mimulus_.

Specific goals of this study were 1) to assess the germination phenology, germination rate, and mode of seed dispersal for each species, 2) to evaluate seedling emergence timing for two rare, endemic species relative to a potential competitor, and 3) to attempt to relate observed germination patterns to life history, habitat, and phytogeography.

## DISTRIBUTION AND BIOLOGY OF STUDY GROUP

The study group is comprised of eight closely related herbaceous species indigenous to arid regions primarily east of the Cascade Mountains (Table 2). _Mimulus moschatus_ and _M. floribundus_ are widespread, polymorphic taxa occurring throughout much of western North America (Grant 1924, Munz 1959, Holmgren 1984). The remaining species are rare or local and exhibit narrower distributions. _Mimulus pulsiferae_ is restricted to the slopes of the Cascadian-Sierran axis, and is most common in northern California. The other five species are geographically centered in eastern Oregon and adjacent Washington and Idaho, with _M. breviflorus_ extending sporadically to adjoining states (Cronquist 1959, Holmgren 1984).

All of the species are genetically self-compatible, ranging from pseudocleistogamous (sensu Vickery 1964, Lord 1981) to facultatively xenogamous (Cruden 1977).

**Table 2.** Life cycle and habitat summaries for individual study species in the <u>Mimulus</u> <u>moschatus</u> complex.

| Species | Life Cycle | Habitat |
|---|---|---|
| <u>Mimulus</u> <u>moschatus</u> Dougl. in Lindl. | Rhizomatous perennial; frequently roots at nodes and capable of sprouting from plant fragments or dislodged rhizomes | Gravel streambanks, well-drained meadows and debris flows; dry during summer months or sometimes wet throughout year |
| <u>M</u>. <u>jungermannioides</u> Suksd. | Perennial via autumn production of over-wintering turions (strobiloid buds) | Restricted to basalt cliff faces in xeric canyons; sites often dry by mid-summer |
| <u>M</u>. <u>hymenophyllus</u> Meinke | Summer annual, or occasionally weakly perennial | Restricted to basalt wall spring sites; dry by mid-summer |
| <u>M</u>. <u>floribundus</u> Dougl. in Lindl. | Summer or winter annual | Gravelly to rocky banks, streambeds, or moist cliffs that dry by early summer |
| <u>M</u>. <u>breviflorus</u> Piper | Summer annual | Gravelly or sandy banks, streambeds, or edges of vernal pools; sites often dry by early summer |
| <u>M</u>. <u>washingtonensis</u> Gand. | Summer annual | Basalt cobbles and exposed bedrock, on well-drained south slopes; dry by July |
| <u>M</u>. <u>pulsiferae</u> Gray | Summer annual | Margins of temporary pools and vernally damp depressions, well-drained sites drying by mid-summer |
| <u>M</u>. <u>patulus</u> Pennell | Summer annual | Restricted to basalt walls and (rarely) rocky riverbanks; sites dry by early to mid-summer |

Individual plants typically produce 30-150 flowers in a
growing season, each capsule capable of generating 50-350
small seeds.

Populations of the species studied are character-
istically isolated and patchy -- they rarely exceed 100
square meters and range in size from a few plants to
several thousand individuals.  Populations usually occur
within vegetation types dominated by species of <u>Agropyron</u>,
<u>Artemisia</u>, <u>Pinus</u>, or <u>Pseudotsuga</u> (Franklin and Dyrness
1973).  Favored microsites commonly shift from a hydric
environment early on to extremely xeric as the growing
season progresses.  The transition from wet to dry is
temporally unpredictable and rapid because the species
frequently occur in exposed situations on rock outcrops or
thin, well-drained soils.  Habitats for all species are
saturated in the early spring, either from pooled
precipitation or inundation by streams or intermittent
springs.  Substrates frequently dry completely by late
spring to mid-summer as waters recede, but may potentially
receive substantial moisture any time during the season,
often from thundershower runoff.  Since flowering
generally continues through at least early summer, seeds
may be shed into a range of fluctuating moisture regimes
as well as subjected to hydration well after initial
release.

Generalized habitat preferences and life cycles of individual species are summarized in Table 2.

## METHODS

Germination trials.--Twenty-two greenhouse populations representing the eight species were established over the winter of 1981-82 in Corvallis, Oregon. Mature plants were grown from previously collected seed, rhizomes, or juveniles transplanted from the field, originating from study sites considered modal with respect to the ecological and geographical ranges of the taxa in the Northwest (see Appendix A). Blooming in the greenhouse commenced in April and May, with sexual maturation of the normally later flowering perennial species accelerated by exposure to an artificial 15-16 hour photoperiod, beginning in late February. The self-compatible but typically outcrossed M. washingtonensis was manually selfed to ensure reasonable seed set.

On 22-23 May 1982, 90-120 dehiscing capsules that had ripened during the preceding week were gathered from each greenhouse population and air dried in paper bags for two days. Samples of at least 2000 seeds per population were stored dry, in covered 9 cm petri dishes, and exposed to natural temperatures and photoperiods outside the greenhouse. On 26 May, two lots of 100 seeds from each population were placed in individual petri dishes, without

filter paper, and immersed under 3-4 mm of distilled
water. Seeds were dusted with Orthocide (50% captan -- N
- trichloromethylmercapto - 4 - cyclohexane - 1,2 - di -
carboximide) to retard fungal growth. Petri dishes were
wrapped in clear plastic film and placed outside under a
lath shadeframe, with water changed every three to four
weeks. Seeds were scored for 1) total percent
germination, through 31 October, and 2) rate of
germination, recorded daily for 30 days, and biweekly
thereafter. Data from the populations were averaged by
species. Identical germination tests were initiated on 19
July and 1 October. All seeds from the July test which
failed to germinate by 31 October were sown on the surface
of moistened potting soil (ca. 80% sandy-loam and 20%
peat) in 15 cm clay pots, and allowed to overwinter. Seed
lots were combined by species, and the eight pots were
kept in a standard cold frame adjacent to the greenhouse.
At this time, 1200 of the remaining 1400 seeds from each
population were stratified by transferring them to
refrigeration, in 3-4 mm of distilled water, at 2 degrees
C. Two lots of 100 seeds per population were subsequently
removed from stratification and placed in the greenhouse
(at 12/20 degrees C min/max) and tested for germinability
after ten days, and then at one, two, three, four, and
five month intervals after initial imbibition. The final
200 seeds per population were stored in dry petri dishes

and left to overwinter in the heated greenhouse. These were irrigated and tested for germinability on 4 April 1983. Seeds from stratified and overwintered lots were scored and averaged, as described previously, through 5 June.

Seed dispersal.--Seed dispersal was observed for greenhouse-grown plants and field populations. Two calyx phenotypes are present in the study group, with both nearly equalling or exceeding the length of the capsule at maturity. One phenotype is characterized by an open, cylindrical calyx tube at anthesis that becomes inflated and urceolate after pollination, developing a conspicuously constricted apex that tends to invest the ripening ovary. The other calyx phenotype is characterized by an open, tubular morphology throughout floral ontogeny. It was hypothesized that the constricted calyces may function in the prolonging or delaying of seed dispersal, either by slowing release due to the narrowing of the orifice, or by trapping seeds between the dehisced capsule and the expanded sides of the calyx tube. To test for a correlation between dispersibility and calyx morphology, 40 pollinated flowers per species were marked and followed to fruit maturation in the greenhouse. The mean seed set was subsequently calculated from 20 of the 40 ripe, undehisced capsules that developed. The remaining fruits were not disturbed, and the plants were

set outside in an exposed area periodically subjected to light to moderate winds. The average number of undispersed seed after 50 days was obtained for each species, and divided by the corresponding mean from seed counts of the unopened capsules. The resulting percentages were normalized by arcsine transformation, with the difference in percent seed retained by the two calyx morphs tested for significance by a t-test.

Seedling emergence timing.--Swift breaking of dormancy and timely emergence of germinants is essential in minimizing the effects of competition from seedlings of other species (Silvertown 1982). Mimulus patulus and M. hymenophyllus are two extremely rare species with apparently rigid habitat requirements (Table 2). Both taxa frequently coexist with the distantly related species Mimulus nasutus Greene, a weedy annual member of the section Simiolus. Observations of the three species in nature revealed similar seedling emergence dates, suggesting that M. nasutus may be affecting recruitment of the rare species. To test for potential differences in seedling emergence times, 1200 seeds of each species were collected from greenhouse plants and stored dry at 20-25 degrees C for four months. Lots of 200 seeds were then sown evenly on potting soil in 15 cm clay pots, and placed unwatered in a lath-covered cold frame on 15 December 1982. Pots were scored daily for cumulative seedling

emergence after initial cotyledon appearance in early February. Scoring continued for 21 days, with the data averaged by species. The seedling emergence curve of M. nasutus was compared to those of M. patulus and M. hymenophyllus by the Kolmogorov-Smirnov procedure, a nonparametric statistic applicable to timing data (Estabrook et al. 1982, Winsor 1983).

Precocious maturation and drought stress.--All of the species studied frequent habitats that are prone to desiccation, potentially subjecting populations to catastrophic seed bank reductions should rapid drying occur after mass germination. An experiment was conducted to evaluate the relative ability of those species lacking innate dormancy to mature and set seed when subjected to post-germination moisture stress. Freshly matured seeds were harvested from greenhouse plants in April 1983, and sown on saturated potting soil in 9 cm plastic pots, 20 for each species. Seeds were watered daily until seedlings were present in all pots. Two seedlings were retained in each container, and selected so that all plants used in the experiment were separated in age by less than 36 hours. After thinning, seedlings were irrigated daily for two weeks. Pots were divided, by species, into two lots, one watered to field capacity every other day, and the other every ten days. Plants were grown in the greenhouse and maintained under a 16

hour photoperiod. Cumulative seedling mortality was recorded thrice weekly for each species. Additional data collected from each control and stressed plant were 1) average number of days required to ripen first capsule, 2) average number of seeds set by first capsule, and 3) number of fruit initiated during the experiment. Nonparametric analyses of variance between control and stressed data sets were calculated by the Mann-Whitney U-test. Observations were concluded 40 days after drought stress was induced.

## RESULTS

Germination.--Results of the germination tests (Table 3) separate the eight species into three groups based on the presence or absence of seed dormancy mechanisms. Most seeds of M. moschatus, M. jungermannioides, and M. floribundus could be germinated immediately or shortly after capsule dehiscence, given moisture and normal growing season temperatures. High germination percentages were repeatedly attained for these taxa for each test date through April 1983, demonstrating an absence of an afterripening requirement as well as a lack of appreciable acquired dormancy, either under a natural environment or after cold-wet stratification. Germination initiated quickly for M. moschatus and M. jungermannioides, continuing at a sustained rate for three to four weeks (Fig. 2A).

Table 3. Mean germination percentages recorded for the _Mimulus moschatus_ complex in 1982-83 germination tests. NG = non-germinated seeds from the 19 Jul 1982 imbibition date, which were overwintered outside on 31 Oct; NS = nonstratified seeds incubated dry in the greenhouse and imbibed on 4 Apr 1983. Percentages of 10% or greater are rounded to the nearest whole number.

| | Natural temperature and photoperiod | | | | | Stratification at 2 degrees C (beginning 4 Nov 1982) | | | | | |
| | Dates imbibed[a] | | | NG[b,c] | NS[b] | Released from stratification on[b:] | | | | | |
| | 26 May | 19 Jul | 1 Oct | | | 10 Nov | 4 Dec | 4 Jan | 3 Feb | 4 Mar | 4 Apr |
| Species | | | | | | | | | | | |
| M. moschatus | 99 | 97 | 88 | 0.2 | 91 | 89 | 79 | 82 | 82 | 88 | 95 |
| M. jungermannioides | 97 | 96 | 89 | 1.6 | 97 | 71 | 66 | 73 | 89 | 96 | 94 |
| M. floribundus | 84 | 92 | 67 | 3.3 | 89 | 87 | 56 | 89 | 99 | 98 | 92 |
| M. hymenophyllus | 93 | 16 | 4.0 | 65 | 6.1 | 0.1 | 2.0 | 70 | 88 | 82 | 90 |
| M. breviflorus | 96 | 0 | 0 | 81 | 0 | 0 | 0 | 16 | 91 | 94 | 88 |
| M. washingtonensis | 0.3 | 0.1 | 0 | 89 | 0.1 | 0 | 0 | 26 | 87 | 90 | 91 |
| M. pulsiferae | 0 | 0.1 | 0 | 76 | 0 | 0 | 0.2 | 14 | 66 | 73 | 76 |
| M. patulus | 0.1 | 0 | 0 | 64 | 0 | 1.0 | 2.4 | 19 | 68 | 50 | 61 |

[a] Germination percentages recorded through 31 Oct 1982

[b] Germination percentages recorded through 5 Jun 1983

[c] Germination percentages to be added to those of 19 Jul for total germination of Jul 1982 test lots
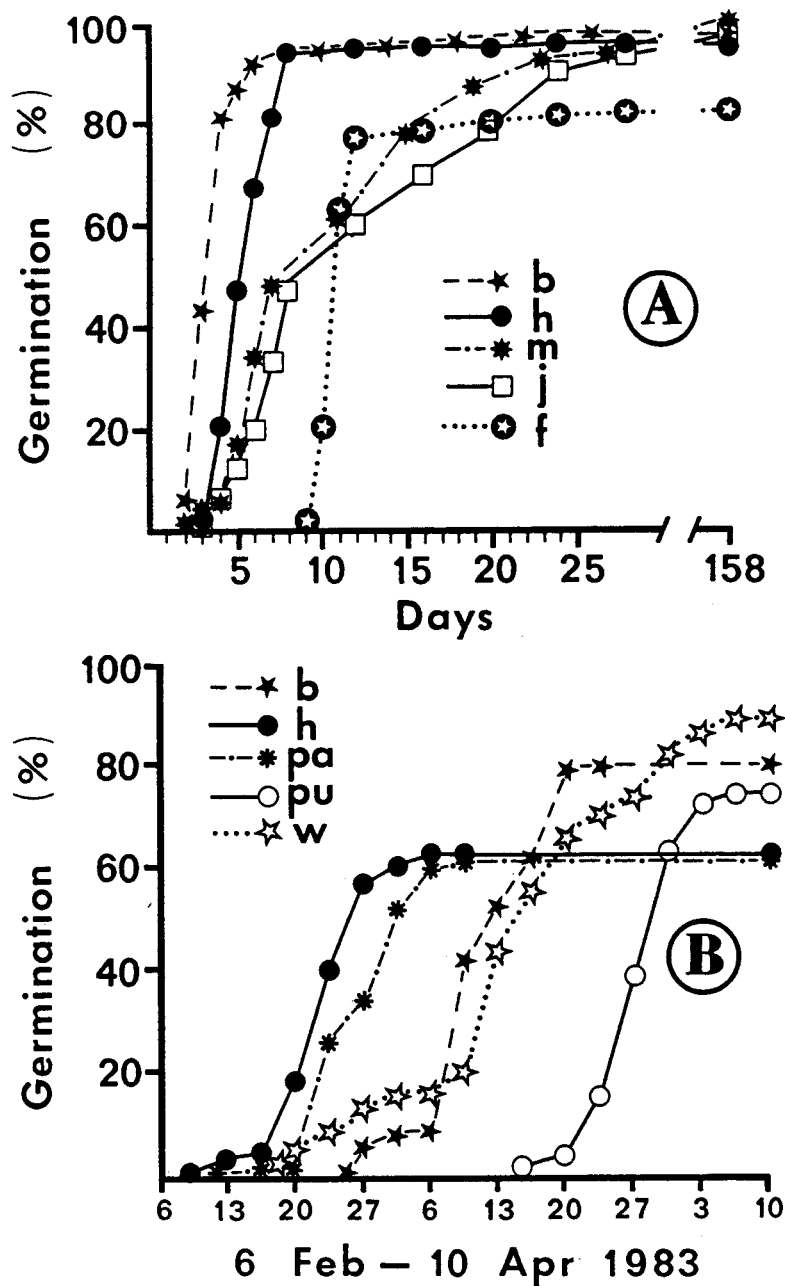
**Figure 2.** Seed germination rates for <u>Mimulus</u> <u>breviflorus</u> (b), <u>M</u>. <u>hymenophyllus</u> (h), <u>M</u>. <u>moschatus</u> (m), <u>M</u>. <u>junger-mannioides</u> (j), <u>M</u>. <u>floribundus</u> (f), <u>M</u>. <u>patulus</u> (pa), <u>M</u>. <u>pulsiferae</u> (pu), and <u>M</u>. <u>washingtonensis</u> (w). **Fig. 2A** illustrates germination rates for nondormant seeds imbibed on May 26 and scored through Oct 31. **Fig. 2B** illustrates rates of germination for dormant seeds from the Jul 19 germination test that were overwintered outdoors, beginning on Oct 31 (see entries under NG in Table 3).

Mimulus floribundus delayed germination for an average of nine days, followed by a comparatively rapid burst, with ca 80% germination occurring in four days (Fig. 2A). A few seeds of each species are apparently capable of delaying germination until the spring following dispersal, even though continually exposed to favorable growing conditions (see column headed "NG", Table 3).

Seeds of M. hymenophyllus and M. breviflorus germinated rapidly in the immediate post-maturation period, achieving 92-95% germination in five to six days (May test, Table 3; Fig. 2A). Subsequently tested seed lots of these species developed complete or partial dormancy prior to 19 July (Table 3). Mimulus hymenophyllus seeds retained limited germinability in the July and October germination tests, while seeds of M. breviflorus were completely dormant. Dormancy was broken in both species following two to three months cold-wet stratification (Table 3). Germinants from seeds that were overwintered outdoors began to appear in early to late February, with emergence rates peaking in 13-15 days and leveling off in 23-25 days (Fig. 2B).

The remaining three species, M. washingtonensis, M. pulsiferae, and M. patulus, exhibit virtually complete innate dormancy. All attempts to germinate seed of these species without a cold-wet treatment resulted in germination of less than or equal to 0.3% (Table 3).

After two to three months exposure to artificially induced
stratification, seeds could be germinated to medium to
high percentages (Table 3). Emergence of seedlings in the
cold frame began in mid-February for M. patulus and M.
washingtonensis, and mid-March for M. pulsiferae (Fig.
2B).

Seed dispersal.--The Mimulus moschatus complex is
characterized by stiffly ascending fruiting pedicels three
to fifteen times the length of the calyx, extending the
erect capsules out and away from the glandular-sticky
foliage. No evidence of animal mediated dissemination was
observed during the study. Ripe seeds are typically
spilled from the dehisced capsules and calyx tubes by
wind, with dispersal from the vicinity of parent plants by
wind or flowing water. The only exception to this pattern
occurs in M. hymenophyllus, an obligate cliff-dweller
known only from sheer basalt walls near the Snake River in
northeast Oregon. One to three days after pollination,
pedicels of this species become negatively phototropic at
the base and also near the point of attachment to the
calyx. As the pedicels grow away from sunlight and
towards the vertical substrate, developing capsules are
positioned for seed dispersal into darkened crevices.
Pedicels of plants grown under lamps in the greenhouse
retained this behavior, consistently orienting capsules
away from the direction of the light.

Collective comparison of species possessing urceolate and cylindrical fruiting calyces showed that seed numbers retained by the former group were significantly higher after 50 days (Table 4). The extremely low retention of seeds by M. hymenophyllus is a result of the pedicel phototropism, which even in greenhouse pots consistently results in rapid self-dispersal. The low retention rate of M. washingtonensis is related to the relatively taller and rigidly erect habit of this species (to 3.5 dm), which subjects plants to greater wind sway. Conversely, the relatively high rate of seed retention of M. moschatus is facilitated by its creeping habit, as well as long, twisting sepal apices which envelop and obstruct the calyx orifice as the tube expands.

Timing of seedling emergence.--Seedling emergence of Mimulus hymenophyllus, M. patulus, and M. nasutus began on 8 February, and was plotted as the cumulative proportion of emergents, by species, during the 21 day sample period. Mimulus nasutus seeds are not dormant (Kiang 1973; Meinke, personal observation), and a few seeds of this species germinated shortly after planting in December. Cold temperatures rapidly killed these germinants and enforced dormancy of the remaining seeds, however, and the 32 seeds lost to premature germination were insignificant to the experiment.

**Table 4.** Parental seed retention of selected <u>Mimulus</u> species
with distally narrowed, urceolate fruiting calyces (U) versus
species with cylindrical, open-ended fruiting calyces (C).
R = the ratio of the means, B/A, where B = the number of seeds
remaining within dehisced capsules and calyx tubes after 50
days of exposure to natural dispersal conditions outside the
greenhouse (n = 20), and A = the number of seeds contained in
ripe, undehisced capsules (n = 20). Comparison of the two
calyx morphs indicates that taxa with urceolate calyces retain
significantly higher amounts of seed through time than those
with open calyces (t = 4.28, P<0.01).

| Species | Calyx morph | A | B | R | arcsin R |
|---|---|---|---|---|---|
| <u>M</u>. <u>moschatus</u> | U | 218 | 187 | .86 | 68.03 |
| <u>M</u>. <u>floribundus</u> | U | 197 | 95 | .48 | 43.85 |
| <u>M</u>. <u>breviflorus</u> | U | 129 | 79 | .61 | 51.35 |
| <u>M</u>. <u>jungermannioides</u> | U | 112 | 46 | .41 | 39.82 |
| | | | | | |
| <u>M</u>. <u>hymenophyllus</u> | C | 77 | 5 | .06 | 14.18 |
| <u>M</u>. <u>pulsiferae</u> | C | 133 | 24 | .18 | 25.10 |
| <u>M</u>. <u>patulus</u> | C | 141 | 30 | .21 | 27.27 |
| <u>M</u>. <u>washingtonensis</u> | C | 119 | 10 | .08 | 16.43 |

The differences between the emergence curves of M. nasutus and the two rare species were highly significant (Fig. 3), with M. nasutus emerging sooner and over a shorter period of time. By observation day 10, 93% of the M. nasutus seedlings that appeared over the 21 days had germinated. Seedling counts for M. hymenophyllus and M. patulus reached this percentage on days 15 and 18, respectively.

Precocious maturation and drought stress.--Young plants of the perennials Mimulus moschatus and M. jungermannioides, and the typically annual M. hymenophyllus, did not develop fruit during the 55 days of observation. Germinants of these species exhibited faster and greater cumulative mortality, particularly when moisture-stressed, than did the annuals M. floribundus and M. breviflorus (Figs. 4A, 4B), which are more common in habitats where summer drought is comparatively early and unpredictable.

Most individual plants of Mimulus floribundus and M. breviflorus set at least one fruit that produced ripe seed, with stressed plants of both species maturing their first capsules significantly sooner than controls (Figs. 4A, 4B; Table 5). Although averaging earlier fruit set, stressed plants developed significantly fewer seeds in their initial capsules than their nonstressed counterparts (Table 5). Twenty-five days after drought was induced,

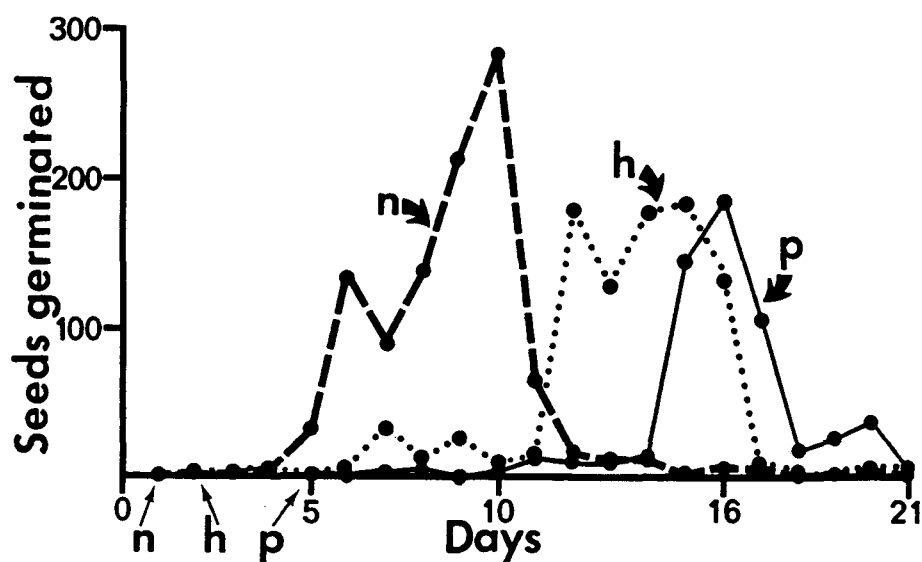**Figure 3.** Germination curves for <u>Mimulus nasutus</u> (n), <u>M.</u> <u>hymenophyllus</u> (h), and <u>M. patulus</u> (p), based on seedling emergence from February 8 through March 1.  Emergence of <u>M. nasutus</u> seedlings was significantly earlier than those of <u>M. hymenophyllus</u> (D = 0.81, m = 1058, n = 929, P<0.01) and <u>M. patulus</u> (D = 0.88, m = 1058, n = 607, P<0.01) [Kolmogorov-Smirnov two-sample test].
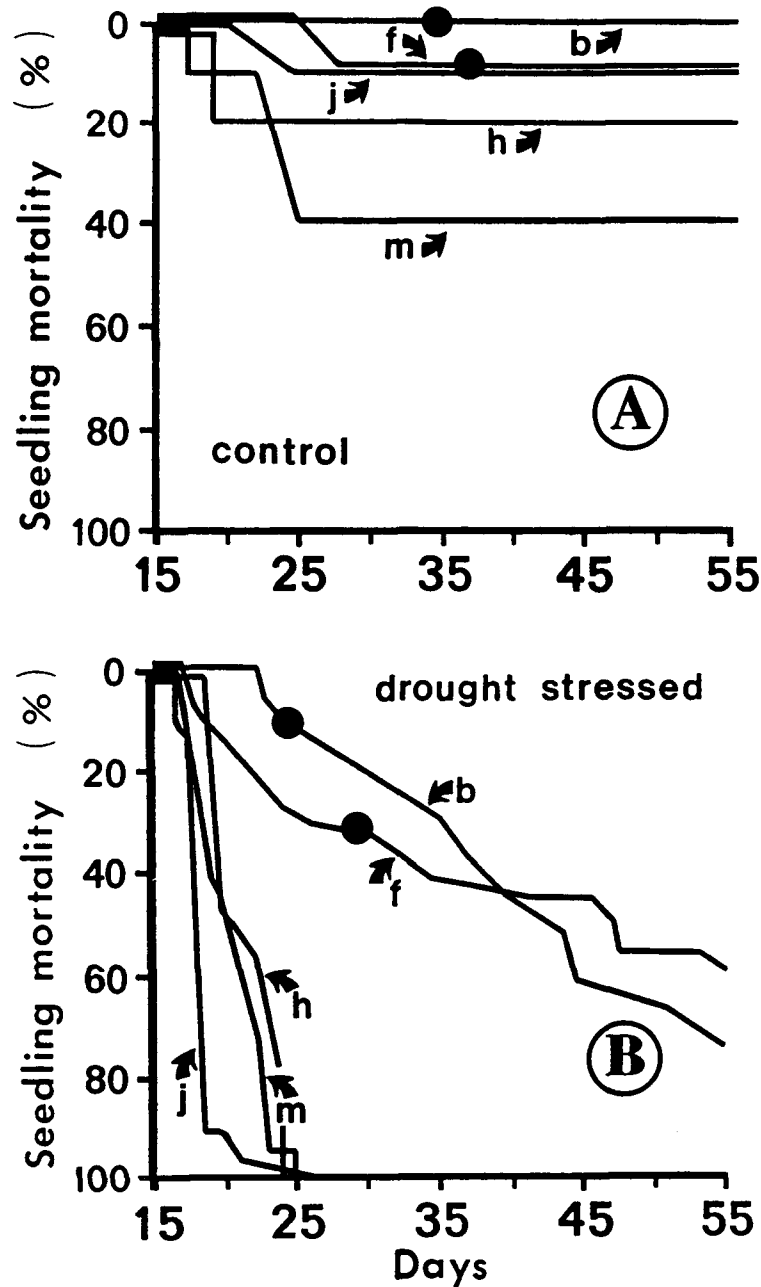
**Figure 4.** Survivorship of fifteen day old seedlings of *Mimulus* species that lack innate seed dormancy [*M. breviflorus* (b), *M. hymenophyllus* (h), *M. moschatus* (m), *M. jungermannioides* (j), and *M. floribundus* (f)]. Cummulative mortality is depicted for control seedlings **(Fig. 4A)**, watered every day, and stressed seedlings **(Fig. 4B)**, watered at ten day intervals. Darkened circles approximate the time of appearance of the first mature capsule.

**Table 5.** Quantitative summary of seed and fruit production of drought-stressed and control plants of Mimulus breviflorus and M. floribundus (n = 20 for each treatment).

| Species | No. of plants producing seeds | Mean days to first ripe fruit | Mean seeds per first fruit | Mean no. of fruit at day: 25 | 40 |
|---|---|---|---|---|---|
| **M. breviflorus** | | | | | |
| Control: | 20 | 40.5 | 125.8 | 1.3 | 2.5 |
| | | * | ** | NS | *** |
| Stressed: | 18 | 35.9 | 71.2 | 1.1 | 1.4 |
| **M. floribundus** | | | | | |
| Control: | 18 | 41.2 | 177.8 | 1.6 | 3.3 |
| | | *** | *** | NS | * |
| Stressed: | 14 | 35.6 | 65.4 | 1.5 | 1.9 |

Differences between treatment means are significant at levels of *P<0.05; **P<0.01; and ***P<0.001 (Mann-Whitney U-test of unequal samples)

the total number of capsules initiated by stressed and
nonstressed populations did not differ significantly for
either species, but by 40 days, controls of both taxa
averaged considerably greater numbers of fruit due to
mortality or growth cessation of stressed plants (Fig. 4B,
Table 5).

## DISCUSSION

Germination patterns.--Three germination patterns
occurred in the Mimulus moschatus complex, comprising
species with and without physiologically-based dormancy
mechanisms.  Innate dormancy is common among plant species
that occur in arid regions or disperse seeds into
unpredictable moisture regimes (Harper 1977, Grime 1979,
Westoby 1981), yet only three of the eight Mimulus species
studied here exhibit this trait.  The other five species
will either germinate throughout the growing season, or
develop seed dormancy after an initial period of post-
maturation germinability.  In the species without innate
dormancy, potential exists for high seedling mortality and
a limited ability to maintain a seed bank.

Physiological adaptations which delay germination
often serve to promote seed bank establishment, buffering
populations from environmental fluctuations.  In M.
patulus, M. pulsiferae, and M. washingtonensis, strong
innate dormancy presumably preserves overwintering seed

pools for spring germination, and maintains local populations via _in situ_ regeneration. Since these species characteristically occur in small, isolated patches (due to edaphic requirements), innate seed dormancy has the added selective advantage of promoting genetic variability and stability by increasing the effective breeding group (Epling et al. 1960, Gottlieb 1974, Baskin and Baskin 1978, Templeton and Levin 1979).

Strict dependence on innate dormancy is relaxed in M. hymenophyllus and M. breviflorus. These species may rapidly germinate freshly ripened seeds during the growing season if provided with adequate moisture and warmth, but may also potentially develop seed banks through induced dormancy if propagules are not imbibed within a short time of capsule dehiscence. Seedlings which establish early in the season may flower and further enhance the seed crop of the current year. Overwintering juveniles, occasionally observed in M. hymenophyllus, may ultimately produce more seed than spring germinants, and may also have a survivability edge in unfavorable years (Arthur et al. 1973, Harper 1977).

Population maintenance of species lacking the insurance of seed dormancy mechanisms necessitates compensation for potentially lethal post-dispersal environments, either through adult morphologic traits or adaptation at the juvenile stage of the life cycle. This

is especially relevant in habitats that rapidly shift between wet and dry conditions during the growing season. Such compensatory traits may serve to delay seed dispersal until the more predictable moisture regimes of early winter or spring, or mitigate the effects of seed crop mortality should germination episodes be followed by unfavorable environmental conditions.

In species producing generally nondormant seed crops, innate dormancy of a few seeds is occasionally detected (Harper 1977). Seeds of M. moschatus, M. jungermannioides, and M. floribundus are overwhelmingly nondormant during the season of dispersal; however, a small fraction (0.2-3.3%) did not germinate until the following spring (NG, Table 3). These observations parallel those of Vickery (1983) in his studies of germination plasticity in Great Basin forms of Mimulus guttatus DC., where approximately 99% of the seeds tested germinated within three weeks, while the remaining 1% remained dormant for a year or longer. Vickery (1983) characterized this delay as a genetically controlled germination polymorphism, acting to maintain small but important seed banks. This conclusion was based on field observations of occasional seedlings germinating in the spring. While observations of M. moschatus, M. jungermannioides, and M. floribundus also revealed sporadic early spring germination, it is not clear to what

extent this is attributable to heritable factors as opposed to simple morphological (see below) or environmental controls.

Relationship of life cycle and morphology to germination.--The fact that seed may ripen in a relatively limited time and also be nondormant does not necessarily imply that it is released and dispersed in a correspondingly short period (Harper 1966, 1977). Four of the five Mimulus species studied here that lack innate dormancy possess floral adaptations that significantly restrict rapid seed dispersal. Besides improving chances for prolonged recruitment by potentially exposing seed crops to a variety of post-dissemination environments, staggered dispersal may also result in parental retention of seed until cold fall temperatures enforce dormancy, particularly if coupled with late season seed production (Amen 1966). Greenhouse and field populations of M. moschatus, M. jungermannioides, and M. floribundus will often ripen seed into late October (Meinke, personal observation), and even fruit developed as early as mid-summer may retain seed sufficiently long enough to contribute to an overwintering seed pool. This suggests that the morphological adaptation of inflated calyces, here implicated in the establishment of transitory seed banks for species lacking innate dormancy, is the primary agent for spring regeneration in average years. A minor

germination polymorphism may result in the limited perennation of a seed pool, as postulated by Vickery (1983), but its role in vernal replenishment of populations is probably significant only in years following very poor growing seasons.

The most reliable hedge against seed crop failure or post-dispersal mortality is perennation of adult plants. _Mimulus moschatus_ and _M. jungermannioides_ commonly propagate vegetatively, thereby mitigating the potentially negative aspects of unrestricted germination due to a lack of seed dormancy. Compared to related annuals, these perennial species exhibit more prolonged germination rates, slower seedling development, and higher pre-reproductive mortality (Figs. 2A, 4B). Successful seedling establishment in the field is uncommon for _M. moschatus_ and _M. jungermannioides_ (Meinke, personal observation), and it may be that recruitment is episodic in these species and related to substrate disturbance, as speculated for the vegetatively spreading bog perennial _Mimulus primuloides_ Benth. (Douglas 1981).

In _Mimulus floribundus_ and _M. breviflorus_, germination may occur throughout the growing season if adequate soil moisture coincides with seed dispersal. In these species, the hazards of releasing nondormant seeds into habitats with unstable moisture conditions are offset by the potential for rapid life cycle completion under

drought conditions (Table 5, Fig. 4B). The ability for precocious maturation enhances the reproductive potential of a seedling cohort, even if germination occurs during a period of increasing soil desiccation. The fact that moisture-stressed plants and controls did not differ significantly in the number of capsules present 25 days after watering was discontinued (Table 5) implies that the rapid rate of fruit and seed set has a genetic basis, and is not simply an environmental response. Initial capsules of plants subjected to stress did, however, ripen significantly sooner and contain fewer seeds than did those of the controls, suggesting that a drying habitat may prompt redirection of resources for a faster reproductive effort at the expense of mean seed output. Other annuals, particularly weedy grasses, are known to react similarly (Newman 1967, Ewing and Menke 1983).

The ability to germinate throughout the growing season facilitates opportunistic recruitment, colonization, and migration, particularly in autogamous plants (Baker 1955), but may also result in possibly catastrophic seedling loss and seed pool attrition from pre-reproductive mortality. Nevertheless, if the success of a species is measured in terms of ecogeographic amplitude, the most effective germination modes in the M. moschatus complex are those that associate the lack of innate dormancy with one or more adaptations to mitigate seedling

loss. The widespread _Mimulus floribundus_ best exemplifies this strategy, combining nondormant seeds and a modified fruiting calyx with classic r-selected traits, including semalparity, rapid development, and high reproductive effort (Gadgil and Solbrig 1972, Baker 1974, Harper 1977, Silvertown 1982). The overall result is a species which, despite a potentially vulnerable absence of seed dormancy, exploits a variety of mostly summer-xeric habitats throughout western North America. A further consideration is the minor germination delay exhibited by _M. floribundus_ (Fig. 2A), which may facilitate long-distance dispersal in water by reducing premature germination during seed transport. Gene flow studies by Waser et al. (1982) confirm the establishment of _Mimulus guttatus_ seedlings derived from water borne seeds up to 400 m from parents, and suggest that dispersal likely occurs over substantially greater distances.

_Seed germination patterns and species rarity_.--In this study, innate dormancy is shown to be possessed by the three annual species of _Mimulus_ that lack specialized means of seed dispersal (i.e., _M. washingtonensis_, _M. patulus_, and _M. pulsiferae_). These taxa are edaphically restricted and rare throughout their geographic ranges, occurring in discrete, disjunct patches in relation to local soil conditions. The accumulation and function of seed banks in these species may be similar to the

situation described for the Tennessee cedar glade endemic
*Leavenworthia stylosa* Gray (Baskin and Baskin 1971, 1978;
Zager et al. 1971), where a large seed pool ensures
continuation, without immigration, of small, isolated
populations.

Five of the eight species studied here have been
considered potentially threatened or endangered (i.e.,
*Mimulus washingtonensis*, *M. hymenophyllus*, *M. pulsiferae*,
*M. patulus*, and *M. jungermannioides*), primarily due to
narrow distributions and limited abundance (Siddall et al.
1979, The Nature Conservancy 1989). While innate dormancy
in the *M. moschatus* complex is strongly associated with
edaphic specialization and endemism, species rarity in the
group is not restricted to any particular germination
strategy. It is interesting that the three rarest
species, *M. patulus*, *M. hymenophyllus*, and *M.
jungermannioides*, are all specific to basalt wall or scree
habitats, yet have strikingly different patterns of
germination and dispersal. Inasmuch as available habitat
for these species is limited and isolated, opportunities
for interpopulational gene exchange are probably minimal
even though flowers are large (15-30 mm) and apparently
adapted for outcrossing in *M. hymenophyllus* and *M.
jungermannioides* (Meinke, unpublished).

Reduced pollen and seed flow and high rates of
autogamy are commonly believed to increase homozygosity

and render narrowly adapted species less capable of compensating for environmental fluctuations (Solbrig 1972, Levin and Kerster 1974, Jain 1976). Although geographic isolation can promote genetic inflexibility, concurrent adaptation to a narrow, yet stable, habitat may facilitate the persistence of localized populations. This is evident in M. hymenophyllus and M. jungermannioides, which have evolved unique traits associated with propagule dispersal. Mimulus hymenophyllus ensures the perpetuation of populations on cliff faces by releasing seeds after negatively phototropic pedicels have oriented capsules towards the openings of darkened crevices. The short, open-cylindrical calyx of this species promotes rapid dispersal, and its comparatively large seeds (0.65-0.85 mm) may be an adaptation to seedling etiolation in the crevices. Mimulus jungermannioides is facultatively clonal, producing turions at the tips of filiform stolons that penetrate rock fissures in late summer. These overwintering buds detach as parent ramets decay, subsequently bolting in early spring. Since shoot origin in M. jungermannioides is over 94% vegetative in nature (Meinke, unpublished), the less specialized mode of seed dispersal and the lack of innate dormancy in this species may be inconsequential to population maintenance.

Although the dispersal strategies of M. jungermannioides and M. hymenophyllus contribute to

overall rarity by restricting emigration, these species are apparently effective in maintaining isolated, local populations. Both taxa probably reduce competition from other cliff species by dispersal mechanisms which enhance propagule arrival in safe sites (Harper et al. 1965). Mimulus patulus apparently lacks this ability due to unspecialized seed dispersal (Table 4), and may therefore be more vulnerable than M. hymenophyllus to competition with sympatric species such as Mimulus nasutus (Fig. 3). Mimulus nasutus is morphologically and ecologically plastic, and colonizes a great variety of habitats (Vickery 1978). It grows directly with M. patulus in mixed populations at all of the known sites for the latter species, typically at several times the density and at a more advanced phenological stage than M. patulus. These field observations concur with the germination curves in Fig. 3. Kiang (1973) suggests that M. nasutus is a recent product of quantum evolution, having radiated extensively after selection for self-pollination and an annual life cycle. Conversely, the isolated occurrences and habitat requirements of M. patulus and its endemic allies are suggestive of relictual distributions. Given these assumptions, M. nasutus could be a relatively recent immigrant to the cliff sites currently inhabited, and perhaps initially colonized, by M. patulus.

The apparent lack of selection by M. patulus for an earlier spring germination phenology, or for summer or fall germination via an afterripening period or delayed dormancy, may relate to limited genetic potential. While there is no empirical evidence to show that the earlier germination and higher densities of M. nasutus actually exert a negative influence on the recruitment of M. patulus, many studies have demonstrated strong competitive interaction between closely sympatric species (Harper 1977, Estabrook et al. 1982), especially when niche overlap occurs in a stable habitat (Gause 1934, Silvertown 1982). Mimulus patulus may be rare simply because it is a relict entity, but it may also be declining or going extinct locally due to unspecialized seed dispersal coupled with encroachment by a competitively superior species.

CHAPTER IV:

SUMMARY AND CONCLUSIONS

Mimulus hymenophyllus is morphologically and
ecologically distinct from all other known Mimulus taxa
and warrants recognition at the level of species. Despite
similarities to M. jungermannioides and M. moschatus, the
evolutionary affinities of M. hymenophyllus are uncertain
and require further phylogenetic investigation. A
comprehensive systematic study of the M. moschatus complex
and related elements in the section Paradanthus,
preferably incorporating molecular techniques, will be
necessary to interpret the relationships of the group.

Germination strategies within the M. moschatus
complex are at least partially related to life history.
Both perennial species in the group (M. moschatus and M.
jungermannioides) have non-dormant seeds when capsules
dehisce. The potential exists for catastrophic loss of
seed crops in these species via germination during periods
of drought and desiccation, but failure of sexual
reproduction is offset by successful vegetative
propagation from rhizomes or turions.

Seeds of the six annual species studied range from
being nondormant at maturity to being completely dormant
when fruits open. Species with strong seed dormancy shed
their seeds soon after capsules dehisce and presumably

develop seed banks in the soil as a buffer against occasional reproductive failure. Species without innate dormancy of seeds mitigate potential seedling loss by dispersing their seeds slowly from inflated, distally constricted calyces. Two species, M. floribundus and M. breviflorus, are further adapted to reproduction under xeric conditions by having seedlings capable of precocious reproduction in response to reduced soil moisture.

Based on ecogeographic amplitude the most successful species in the M. moschatus complex are those that combine flexibility in timing of seed germination, specialized seed dispersal, and precocious maturation. Of the species studied, Mimulus floribundus apparently has the more efficient combination of life history strategies, and is distributed from Canada to central Mexico in numerous summer-xeric microsites despite the lack of seed dormancy. Rare species such as M. patulus may be at a relative disadvantage due to rigid germination requirements and unspecialized seed dispersal. Seed dormancy may help maintain tiny populations in narrowly defined habitats such as cliff faces; however, small population size may limit genetic diversity and thereby reduce the capability of rare species to select more advantageous germination phenologies in response to niche overlap with competitors such as M. nasutus.

The recent discovery of _Mimulus hymenophyllus_ in Wallowa County underscores the limited extent of our knowledge regarding the geographic distribution and taxonomic diversity of the _Mimulus moschatus_ complex. Our understanding of the biology of this group of species is even less clear. The present research, focusing on the germination attributes of _Mimulus moschatus_ and its uncommon relatives, is the first to examine collectively a complex of rare species of the genus in an ecological context. A few studies have focused on the genetics of some common _Mimulus_ taxa, but there have been no previous attempts to evaluate life history characteristics experimentally in order to facilitate attempts at preservation. The data provided in this thesis on germination requirements and phenology will be valuable should any of the rare species studied become further compromised in the wild. Complimentary information on seed predators, pollinators, breeding systems, genetic diversity, and rates of vegetative propagation (for perennials), is needed to enhance our knowledge of the natural history of the group.

Investigations that go beyond traditional floristic inventories of rare species are a necessity in order to assess the potential for species extinctions. In the Pacific Northwest, projects by Fredricks (1986), on _Calochortus howellii_, and Kaye (1989), on _Astragalus_

<u>australis</u> var. <u>olympicus</u>, are among the few that provide meaningful data concerning the population demographics, reproductive biology, and predation levels of endangered species. Biological studies of a taxonomic complex that includes more than one rare species, such as the <u>Mimulus moschatus</u> group, are a particularly time and cost effective means of collecting conservation-oriented information. The results of such analyses can be integrated with descriptive information on habitat and geographic range and applied within an appropriate management framework.

The potential for accelerated global warming due to the "greenhouse effect" is a compelling reason to focus on understanding the interactions between rare plants and their environment. Distributional studies alone cannot generate the level of accurate forecasting needed to design long-term policies concerning endemism, bio-diversity, and endangered species management in relation to climatic changes. Species-specific knowledge of population genetics and selected life history traits, such as germination and seedling ecology, will become increasingly valuable in estimating the adaptive amplitude of rare taxa and narrow endemics under altered environmental conditions. The research by Fredricks (1986) and Kaye (1989), and the taxonomic and ecologic studies of <u>Mimulus</u> presented here, are examples of

approaches that might be employed in developing comprehensive conservation plans for endangered or otherwise sensitive plant species.

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# APPENDIX

**Appendix A.** Field Sites Used in the Collection of Mimulus Species for Establishment of Greenhouse Populations.

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**Species listed below were established in the greenhouse from either rhizomes, seeds, or transplanted seedlings, indicated by (a), (b), and (c), respectively.**

(a) Mimulus moschatus. OREGON: Wallowa Co., above Horse Creek, ca. 10 km south of its confluence with the Imnaha River; Grant Co., along sandy edge of Stony Creek, ca. 0.8 km north of the John Day River, ca. 19 km west of Dale; Union Co., ca. 3.0 km northwest of Catherine Creek State Park, between county road and Catherine Creek.

(b) M. jungermannioides. OREGON: Wasco Co., along Bakeoven Creek on east aspect of weathered basalt, ca. 2 km southeast of the Deschutes River; Gilliam Co., above Interstate 84, ca. 7.2 km east of the Sherman Co. line; Umatilla Co., ca. 8.0 km west of Rieth, on south-facing aspects above the Umatilla River.

(b) M. hymenophyllus. OREGON: Wallowa Co. (two sites), above Horse Creek, ca. 12, and, ca. 17 km south of its confluence with the Imnaha River.

(b) M. floribundus. WASHINGTON: Walla Walla Co., rocks above the Columbia River, ca. 6 km northeast of the Oregon state line; Whitman Co., ca. 8.0 km south of Wawawai, on basalt cliffs above the east side of the Snake River. OREGON: Wasco Co., in dried streambed along Bakeoven Creek, ca. 2.5 km southeast of the Deschutes River.

(b) M. breviflorus. OREGON: Baker Co., above high water mark along west side of Higgins Reservoir; Wasco Co., dried vernal pool beds in sand dunes, along the Columbia River near Mosier; Harney Co., vernally moist depressions near the Blitzen River, ca. 6 km southeast of Frenchglen.

(c) M. washingtonensis. OREGON: Grant Co. (two sites), above North Fork of the John Day River, in dry alluvium ca. 14 km west of Dale, and, ca. 16 km south of Dayville, along dried rivulets above the South Fork of the John Day River; Wheeler Co., in rocky field above the John Day River, ca. 12.5 km east of Service Creek.

(c) M. pulsiferae. OREGON: Jefferson Co., 1 km northwest of Camp Sherman along dry creek bed. WASHINGTON: Klickitat Co., dry fields in the vicinity of Glenwood.

**(c) M. <u>patulus</u>.** OREGON: **Wallowa Co. (three sites),** along Horse Creek, ca. 13, **and,** ca. 15 km south of its confluence with the Imnaha River; **also** along Oregon State Highway 3, on cliffs ca. 1 km south of the Washington state line.