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AN ECOLOGICAL STUDY OF THE REGIONAL ENDEMIC
PENSTEMON LEMHIENSIS (KECK) KECK & CRONQ. (SCROPHULARIACEAE)

By

Jennifer Ramstetter

B.S., Marlboro College, 1981

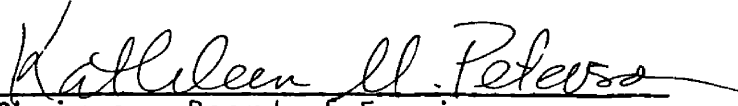
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1983

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An Ecological Study of the Regional Endemic Penstemon lemhiensis
(Keck) Keck & Cronq. (Scrophulariaceae) (117 pp.)

Director: Kathleen M. Peterson *Krup*

Patterns of species distribution and abundance have long been of interest in ecology. Aspects of occurrence such as rarity and endemism have received recent attention in conservation efforts also; information on the biology of rare plants is essential when proposing species conservation measures. Data from rare plant studies suggest that the causes of rarity are diverse and merit investigation for all types of rare species.

This study focused on the ecology of the regional endemic Penstemon lemhiensis. The species is restricted to southwestern Montana and adjacent Idaho and exhibits a patchy distribution within this range. Included in the study are qualitative and quantitative investigations on 1) habitat characteristics, 2) population size and structure, 3) reproduction, 4) competition, and 5) predation. Most of the native habitat of P. lemhiensis consists of relatively dry sagebrush hillsides; the slopes are generally steep and south-facing. Populations in this habitat are often small and isolated from one another. Three of six populations visited have fewer than one hundred individuals concentrated in one central area. In terms of reproduction, the species is essentially an obligate out-crosser. Insect pollination is probably effected by several Hymenopteran species, and a Vespidae wasp may be a particularly important pollinator. Seed production appears to be somewhat limited by pollinator abundance or activity. However, seed production probably does not severely limit population size when adequate seedling establishment sites are available. Penstemon lemhiensis exhibits characteristics of ruderal species; it occurs infrequently in areas of dense vegetation, and often colonizes sparsely vegetated disturbed sites. Associated species occur in both sparsely and densely vegetated areas. Predation on inflorescence stalks at all locations may reduce the level of seed production. Deer, cattle, and insects contribute to herbivory damage.

The ecological aspects studied may in part explain small and isolated populations characteristic of Penstemon lemhiensis. These factors are likely to be less significant in creating the restricted geographic range exhibited by the species. The evolutionary history and genetic make-up of the species may be more important in this regard. Experimental manipulation and comparative studies of P. lemhiensis and closely related, widespread species are essential to fully evaluate rarity. Penstemon lemhiensis should be considered threatened throughout its range. Preservation of undisturbed sagebrush hillsides is perhaps most critical in reducing further threats to the species.

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Al Schultze, Superintendent of the Big Hole National Battlefield, provided the opportunity to use the Battlefield as my primary research location. Jane Bardolf graciously shared her living quarters during the summer and continues to share her delightful friendship with me.

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Dedicated with love to Dr. Robert Engel who weaves his extraordinary knowledge of natural history and scientific precision into ecology. What I have learned from him has influenced every phase of my research.

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CHAPTER I

INTRODUCTION

Species exhibit a wide array of distribution and abundance patterns. Naturalists and ecologists have devoted much of their time to documenting species' boundaries and understanding why they exist as they do. During their travels in the 1800's, Charles Darwin and Alexander von Humbolt were among the first to encounter both narrowly endemic and cosmopolitan species. Darwin noted the climatic regimes that determine the broad boundaries of species' ranges, and he recognized that biological interactions, as well as physical processes, affect where a species is found and its frequency of occurrence.

As the science of ecology developed in the early 1900s, interpreting the distribution of plants was perhaps the most active area of inquiry by botanists (Worthington 1982). At this time, Joseph Grinnell and other naturalists were cataloging the distributions of hundreds of animal species including birds, mammals, and reptiles. Works such as "Geographical Distribution of Plants in Relation to Climatic Factors" (Salisbury 1926) emphasized the role of abiotic factors. Similar principles were applied in The Distribution and Abundance of Animals (Andrewartha and Birch 1954). In the next few decades, ecologists began to focus more attention on the idea that interactions among plants

and animals are important and may affect species' distributions. In Geographical Ecology, MacArthur (1972) synthesized current thought on the subject--much of it his own--and illustrated the influence of climate, history, habitat, genetics, competition, and predation with numerous plant and animal examples.

THEORETICAL TREATMENTS OF RARE SPECIES

Rarity is one aspect of distribution and abundance that has stimulated debate among ecologists. Why are some species localized and/or represented by few individuals while other species are widespread and/or abundant? What is the biological basis of these extreme types of distribution? Answers to these questions have been sought in the evolutionary history, genetic make-up, and ecology of rare species.

Rare species represent a portion of a continuum from exceedingly restricted and infrequent species to common and widespread species. The terms rare and common are not easily defined except in a comparative sense, and there have been a variety of attempts to categorize rare species in this way. Mayr (1963) identified three general types of rarity: 1) species restricted to a very few localities, but found in large numbers at those localities, 2) species distributed in many suitable areas throughout its geographic range, but in very low numbers in each area, and 3) species restricted to widely scattered localities over a large geographic area, all of which seems to be suitable habitat. Rabinowitz (1981) presented a theoretical framework that describes eight different types of rare plants as defined by aspects of range, habitat specificity, and local abundance. Ayensu (1981) and Good and Lavarack (1981) discussed

interpretations of degrees of rarity that are employed when identifying rare plant species for conservation programs in the United States and Australia respectively. A theme common to these and other rare species classifications is that "rare" and "common" are relative terms. Although designating categories is useful, the exact nature of distribution and abundance must be stated clearly when classifying a plant as rare.

Early theoretical treatments of species rarity focused primarily on single causes. For instance, Willis (1922) contended that rare species are the products of recent speciation events and have not had time to spread. Others have countered that theory with the idea that rare species are actually relicts with diminishing ranges (Stebbins 1980). Griggs (1940) proposed that rare species are geographic outliers which are competitively inferior to their widespread counterparts. Stebbins (1942) hypothesized that rare species possess little genetic variability, while more common and widespread species are genetically diverse.

These ideas, particularly those based solely on historical and genetical causes, have fallen into disfavor recently. Stebbins (1980) and Drury (1980) pointed out that there is little consistent correlation between rarity or localized distribution and historical age of plant species. Evidence from a survey of many rare plant species indicates

that they may be young, ancient, or intermediate in age. As more data from electrophoretic studies on genetic variability are obtained, it appears that some rare plant species have little genetic variability, while others have high genetic variability when compared with more common species (Stebbins 1980; Drury 1980). Further, depleted gene pools are found in widespread, largely self-fertilizing species, as well as in rare species (Stebbins 1980).

From the acknowledgement that one single factor cannot account for all known rare species, more synthetic theoretical views have emerged. Rabinowitz (1981) noted that perhaps the most common conclusion to be reached at a symposium on rare plant conservation was that there are many sorts of rare species. This is probably the case because they became rare by several different pathways. Stebbins (1980) concluded that three major factors must be considered for each rare species: 1) the past history of populations, 2) ecological factors, and 3) the genetic structure of populations. The third factor encompasses the total amount of genetic variability, the amount of variability released at any one time, and especially the amount of variability present for characters concerning seed production, seed dispersal, and seed size. Although Drury (1980) favored the idea that the biological habitat and the distribution of that habitat will have the maximum effect on the

distribution and abundance of rare plants, he also stated that a great variety of explanations may be important for different types of distribution in both rare and common species. He listed predators and pathogens and the competitive abilities of rare species as potentially important controlling factors in populations.

Harper (1981) emphasized that rarity in plants is a phenomenon in both space and time; important parameters are enumerated below:

Abundance through time as determined by: 1) frequency of disasters; 2) potential for recovery from disturbances (reproductive capacity of the plant species); 3) longevity of the seed bank; and 4) rate of change of the carrying capacity of the environment.

Abundance in space as determined by: 1) size of habitable sites; 2) number of habitable sites; 3) carrying capacity of habitable sites (dependent on length of life and size of individual plants; 4) time for which a site remains habitable; 5) dispersal to habitable sites; and 6) effect of predators and pathogens once established in habitable sites.

EMPIRICAL STUDIES OF RARE PLANT SPECIES

Recent empirical studies on rare plants describe and, less often, test many of the ideas set forth in these theoretical treatments of rarity. Examples reviewed here are divided into five general categories: 1)historical--species age/climatic change, 2)ecological islands, 3)reproduction, 4)predation, and 5)competition. My review is intended to exemplify how biologists have interpreted the role of these factors in determining plant species rarity; other pertinent studies of similar content are not mentioned. Reference to such studies can be found in the papers discussed here.

Historical--Species Age/Climatic Change

There are several known examples of localized species that are thought to be from a few hundred to a thousand years old. Stephanomeria malheurensis (Asteraceae) is represented by fewer than 250 individuals at a single locality in eastern Oregon. This population is at the periphery of the range of another Stephanomeria species that is widespread and ecologically diverse. Individuals of the two species grow interspersed at the locality, and evidence indicates that S. malheurensis arose recently through sympatric speciation (Gottlieb 1973). Clarkia lingulata (Onagraceae) is known from only two sites in the Merced

River Canyon of California at the southern extension of the range of the widespread C. biloba. Chromosomal evidence indicates that C. biloba is the parental species (Gottlieb 1974). At the other end of the spectrum, an example of a restricted, relictual species is Sequoiadendron giganteum (Pinaceae). The redwood, now restricted to coastal northern California, was widespread during the Tertiary in western North America (Raven and Axelrod 1977). A change in the climate in central Mexico is presumably responsible for the contraction of the range of a mangrove, Pelliciera rhizophorae (Ternstroemiaceae). In the Oligocene period, this mangrove extended northward to central Chiapas in Mexico; palynological data suggest that there was an extensive mangrove vegetation comprised of several species at this time. Examination of the strata suggest that the beds were deposited along a coastline of shallow tropical sea with occasional shoreline fluctuations (Langenheim et al. 1967). Such brackish conditions required by mangroves no longer exist in central Chiapas, and P. rhizophora now extends northward only as far as the Pacific coast of Costa Rica (Rabinowitz 1981).

Ecological Islands

Stebbins (1980) cited unusual soil types as the most common factor in creating ecological islands which may be colonized by rare plant species. The restriction of Eriogonum apricum (Polygonaceae) to a ten mile by two mile stretch of highly sterile soil in the Sierra Nevada of California may be an example of this phenomenon (Myaitt 1968, cited in Stebbins 1980). Similarly, Streptanthus glandulosus (Brassicaceae) is found only on serpentine outcrops. The species is widely distributed in the coast ranges of central and northern California, but the populations are spatially isolated from one another due largely to the scattered distribution of the outcrops (Kruckeberg, 1957).

In addition to specific characteristics such as soil type, ecological islands may exist in a broader sense. Skinner et al. (1983) examined 20 characteristics of glade areas (openings in forested habitats) in Missouri where three rare plant species occur. The occurrence of the three species was most closely correlated with glade size, site litter depth, site soil depth, and glade soil depth.

Reproduction

Various aspects of reproduction (dispersal, unusual reproduction requirements, and high seedling mortality in particular) have been implicated in the rarity of some plant species. Stebbins (1980) suggested that the most conspicuous difference between the ecologically similar Cupressaceous genera Juniperus and Cupressus in the western United States is their means of seed dispersal. The seeds of Juniperus are contained in fleshy, berry-like cones that are consumed by birds; thus, seeds may be dispersed in areas beyond the parental plants. In contrast, Cupressus seeds are enclosed in hard, woody cones which simply drop to the ground when ripe. This difference may in part explain why species in the genus Juniperus are widespread, while the genus Cupressus has a higher percentage of localized species than any other woody genus in North America.

Specific physical conditions required during reproduction may predispose some plant species to rarity if those conditions are not consistently present. Notable examples include species which are dependent upon naturally recurring fire to complete their lifecycles. Staavia dodii (Bruniaceae), found only at one nature reserve in Africa, requires fire for germination, but because it is at least 10 years before the plants mature, frequent fires, as well as lack of fires, are detrimental to the species. Moll and

Grubb (1981) proposed that recent changes in fire frequency have contributed to the decline of the species. Orothamnus zeheri (Proteaceae) is another slow-maturing, fire-dependent species restricted to the Cape of South Africa. Critically endangered in 1968, its populations have been greatly increased by deliberate burning (Boucher 1981).

From the plant population studies that have been completed, Sagar and Mortimer (1977) reached the conclusion that the greatest numerical losses for wild plants occur from the point of seed production to seedling establishment. This pattern is evident in rare plants that have been investigated also. Low seedling establishment, rather than low seed output, seems to be most important in limiting population size. For example, the limiting phase of the life cycle of Peucedanum palustre (Apiaceae) seems to be high mortality of seedlings. The study was conducted in the fens of eastern England where the species is at the periphery of its range. Seed production and dispersal, size of the soil seed bank, germination and establishment, and the survival of seedlings and established plants were all investigated (Harvey and Meredith 1981).

Predation

The controlling effect of predators and pathogens on plant populations is best documented in the case of widespread, introduced species. The introduction of the moth Cactoblastis cactorum reduced dramatically the size and number of Opuntia stricta (Cactaceae) populations (also an introduced species) in Australia (Holloway 1964). A similar situation exists with the weed Hypericum perforatum (Hypericaceae) and the beetle Chrysolina quadrigemina that was introduced to control the weed in western North America (Holloway 1964). Another frequently cited example is the fungal pathogen responsible for the decline of the American Chestnut Castanea dentata (Fagaceae) in its native habitats (Nelson 1955).

The extent to which predators and pathogens contribute to rarity in native plant populations is not well documented. Harvey and Meredith (1981) suggested that seed predation on the relatively large seed crop of Peucedanum palustre may contribute to low population densities also. However, they stated that high seedling mortality mentioned previously is a more important factor than seed predation. Greig-Smith and Sagar (1981) found that small mammals preyed heavily on the seeds of Carlina vulgaris (Asteraceae) and depleted the seed source where it is locally uncommon on sand dunes in England. By adding additional seeds to dune

areas, they were able to increase the size of populations. Ward (1981) observed an area in southern England where Juniperus communis is rare and noted that few seedlings grew in the area; rabbits are abundant grazers on the seedlings at these sites. When the viral disease myxomatosis eliminated rabbits in the area, colonization by young junipers was successful for several years.

Competition

The degree to which competition structures populations and communities is an area of active investigation; there are still few examples where competition has been demonstrated through experimental manipulation. For plants, competition has been implicated especially in the production of toxic chemicals that inhibit the growth of nearby plants and in the species turnover that is apparent in succession. Often the exact plant species involved in competitive interactions or the resources for which they are competing are not known with certainty. For example, Noble (In Williams 1981) concluded that competition from surrounding vegetation inhibits the success of Nitraria billardieri (Zygophyllaceae) seedlings. Permanent plots were placed over natural stands of seedlings; some plots were weeded, while others remained as unweeded controls. Forty weeks after weeding, 20% of the seedlings had died in the weeded plots, as compared to 96% mortality in the unweeded plots.

The nature of competitive abilities in rare plants is not well documented, but Drury (1980) summarized thought on the subject by hypothesizing that rare plant species may be tolerant of stressful physical conditions while being poor competitors. Prince and Hare (1981) attributed rarity in the annuals Lactuca saligna (Asteraceae) and Pellicaria vulgaris (Asteraceae) to their inability to occupy areas of high vegetation density. Seedling populations of Bellis perennis, a localized species in England, were increased more effectively by management of the surrounding vegetation than by increased seed production (Foster 1964, cited in Greig-Smith and Sagar 1981). Ward (1981) suggested that the gradual decrease in seedling establishment of Juniperus communis in the study already mentioned might have been due to increased competition from newly established plants.

RECENT TRENDS IN RARE PLANT STUDIES

The fact that several processes may govern the distribution and abundance of plants is further exemplified in a survey of 17 angiosperms rare in the semi-arid regions of Victoria, Australia. Parsons and Browne (1982) evaluated the potential importance of all five factors reviewed here. Two species are rare in Victoria, but common in inland Australia; their rarity in Victoria may be due to the comparative absence of areas of appropriately dry climate. Four species are restricted to small, widely scattered areas

of gypseous soils. Three species require periods of exceptionally high rainfall or extensive flooding before they reproduce successfully; these climatic conditions are themselves rare. Five species are pioneers after fire or clearing; they are not present once vegetation densities become high. The remaining four species lack any of the above characteristics that may be associated with rarity, and were not studied in any detail. However, they are members of genera with high palatability and may be subject to extensive herbivory.

Although the work of Parsons and Browne (1982) reflects a recent trend of considering multiple factors in rare plant studies, these multiple factors were not studied thoroughly in a single species, but rather in several species. Once a potentially important factor was identified, the rarity of the species was attributed to it. It is essential to study all potentially important factors because more than one is likely to be operating for each species. For instance, in the seemingly clearcut example of restriction to soil type, competition may also play a role. When freed of competition, Streptanthus glandulosus was able to grow on non-serpentine soils (Kruckeberg 1951). Rather than having a strict requirement for serpentine soils, S. glandulosus may have a requirement for low competition levels; few other species could tolerate the high magnesium levels

associated with serpentine soils. In her study of three rare plants in glades in Missouri, Skinner (1979) acknowledged that the occurrence of the species in areas with particular characteristics is simply a correlation and that experiments are needed to demonstrate that the species indeed require those habitat conditions. One study where other possible variables were eliminated is Greig-Smith and Sagar's (1981) work with Carlina vulgaris. They controlled for lack of appropriate establishment sites and nutrient deficiencies, and concluded that lack of propagules, probably through predation, was the factor limiting population sizes. Other workers (Harvey and Meredith 1981, Foster 1964, and Ward 1981) have discussed multiple factors to a limited extent also.

Beyond the necessity of demonstrating causation, encountered by all ecologists, ecologists studying rare plants must contend with another serious difficulty: are characteristics associated with rarity unique to or especially well developed in rare species or are they also found in closely related, common species? Although predation may appear to be severe or reproduction inefficient at some stage for a rare plant, these factors may also be characteristic of common species. For example, high predation levels and low levels of seedling establishment are well known in many species, both rare and

common. Stebbins' (1980) comparison of the ecologically similar genera Juniperus and Cupressus is an example of the comparison of a broadly distributed group with a narrowly distributed group. Work that is still in progress on rare and common species of Calochortus (Liliaceae) indicates that there are differences in reproduction and herbivory for these groups (Fiedler, 1983).

Further investigations of rare plants are needed to clarify and test the theories that have been developed during this century. Over a decade ago, MacArthur (1972) remarked that "the patterns of single species' ranges still seem to be catalogs of special cases." To a large degree, this is true for rare plant species even today; although numerous themes have emerged, more empirical data are needed. Rarity remains an intriguing ecological problem.

Rarity is also of great interest in plant conservation efforts. Those plant species that are least abundant and have the most restricted distributions often become endangered and may have accelerated extinction rates due to human impacts. In reviewing the current literature concerned with plant conservation, much of the work emphasizes inventories of rare plant species, general descriptions of their habitat requirements and potential threats to populations. Fewer studies include detailed ecological work. Some of the early stages of developing a

biologically sound framework for conservation efforts are documented in The Biological Aspects of Rare Plant Conservation (Synge 1981, ed.). Frankel and Soule' (1981) stressed the importance of understanding the genetic processes which affect species survival and adaptation in Conservation and Evolution. It has become increasingly clear that conservation efforts must incorporate knowledge of the genetic implications for small and isolated populations. While it is generally agreed that habitat conservation is the single most important factor in conserving species, Watkinson (1981) noted that, as habitat is destroyed, it becomes increasingly important to know how population size is regulated within the remaining portions of habitat. Harper (1981) proposed that information on the critical aspects of population biology in rare plants can even be used to increase population densities.

PENSTEMON LEMHIENSIS

Clearly, it is not possible to generalize the cause of rarity from one species to another, nor is it possible to propose general conservation measures for all rare species. Rather, basic biological information and empirical evidence on the nature of rarity must be gathered in each particular case. Penstemon lemhiensis (Keck) Keck and Cronq. (Scrophulariaceae), endemic to southwestern Montana and adjacent Idaho, provides an interesting opportunity to study

the biology of a rare plant species and to investigate the nature of rarity.

Species Description and Status

Penstemon lemhiensis is a tap-rooted perennial herb with stems approximately 4 dm tall when in bloom. The attenuate cauline leaves seldom exceed 2.5 cm in width and range from 3.5 to 10 times as long as wide. Mature plants usually produce from 1 to 6 inflorescences, each with 20-60 deep blue flowers. Corolla tube length ranges from 28-34 mm; internally the corollas are characterized by a lighter blue region at base of the tube. Four functional stamens and one glabrous staminode are adnate to the corolla tube. The hispidulous anther sacs are 1-3 mm long, and the gynoecium has a superior, two-carpellate ovary. The fruit is a septicidal capsule which contains 20-40 unornamented seeds. Plants begin to flower in late June, and most have mature fruits and seeds by early August.

Penstemon lemhiensis is a member of the subgenus Habroanthus Crosswhite, section Glabri (Rydb.) Pennell, series Speciosi Crosswhite. Closely related species in this subgenus include P. speciosus and P. cyaneus. Penstemon lemhiensis differs morphologically from these two species primarily in characteristics of the calyx, corolla, and stamens. The three species also appear to have

geographically distinct ranges. P. speciosus is widespread in the Pacific coast states and appears to exhibit great ecological amplitude. Plants occupy a variety of dry habitats from valley edges to the upper subalpine regions of the Great Basin Ranges (Holmgren 1982, pers. comm.). The range of P. speciosus extends westward to southwestern Idaho, approximately 200 km east of P. lemhiensis (Keck 1940). Penstemon cyaneus occurs to the east of P. lemhiensis in Madison County, Montana and Park County, Wyoming and to the west in Bingham, Butte, Elmore, Custer, and Lemhi Counties, Idaho (Hitchcock et al. 1969). The smallest gap between the two species is probably 17 km (Henderson 1981, pers. comm.). The relationship among these three species has not been studied. Hitchcock et al. (1969) describe members of the subgenus Habroanthus as being superficially similar, but technically distinct species with hardly overlapping ranges. Keck (1957) suggested that P. lemhiensis arose from the hybridization of P. speciosus and P. cyaneus followed by the separation of the two parental species.

Presently, Penstemon lemhiensis is known from Beaverhead County, Montana and Lemhi County, Idaho. As well as the type locality in Lemhi County, the species has been reported from 17 other locations in Idaho (Henderson 1981). In Montana, there are six reported locations, but only four

of these have been verified in recent years. Keck and Cronquist (1947) cite specimens that were collected in Ravalli County, Montana, but no populations were located there by Watson (1976) or by myself in 1983. The populations verified in Montana are located in the Big Hole River Valley and in the Beaverhead, Anaconda-Pintlar, and Pioneer Mountain Ranges. Across the Beaverhead Mountains in Idaho, P. lemhiensis occurs west and south of Salmon in the Salmon River Mountains and south to the Leadore area (Henderson 1981, pers. comm.) (Fig. 1). The elevation ranges from about 1,200 to 2288 meters in these areas (Henderson 1981). Penstemon lemhiensis grows on steep sagebrush slopes below Douglas fir forests and, particularly at higher elevations, in more level sagebrush areas. Additionally, P. lemhiensis colonizes disturbed sites such as roadcuts and ditchbanks. In all, several thousand plants are known from Montana and Idaho. However, many populations are threatened by cattle grazing, range improvement, and road building and improvement. The spraying of herbicides has eliminated at least one roadside population in Idaho (Henderson 1981).

Penstemon lemhiensis was included in Category I ("currently under review") on the Federal Register of species proposed for listing as threatened or endangered (15 December 1980). As of 27 July, the species was not among

Distribution of Penstemon lemhiensis

All Reported Locations within Range



1. Battlefield, MT
2. Argenta, MT
3. Badger Pass, MT
4. Lemhi Pass, MT
5. Bannack Pass, ID
6. Colson Creek, ID

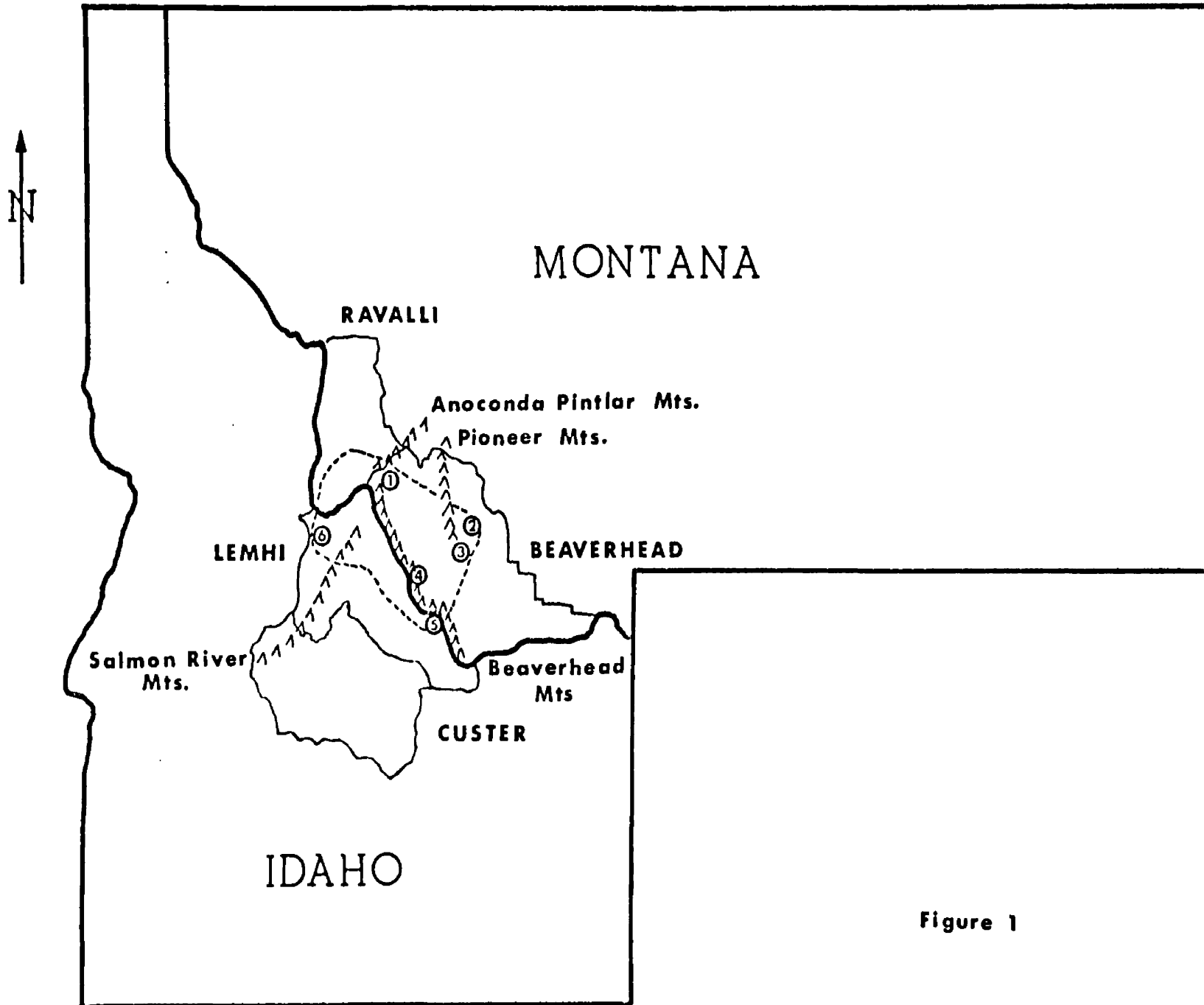


Figure 1

the 67 plant species officially listed as threatened or endangered in accord with the Endangered Species Act of 1973. The Montana Nature Conservancy considers P. lemhiensis to be rare and possibly threatened in Montana. Penstemon lemhiensis was treated as a threatened species in the Bulletin of Vascular Plants of Concern in Idaho (Henderson 1981). The species' status was unchanged in the 1983 Update report.

Study Objectives

Although Penstemon lemhiensis has received attention at both the federal and state levels as a rare plant, no detailed biological studies of the species existed prior to the present study. The major goals of my study were to provide information on the ecology of P. lemhiensis and to elucidate factors that may limit its distribution and abundance. The major objectives of this study included:

- 1) Characterization of the habitat.
- 2) Description of the general size and structure of populations.
- 3) Investigation of the reproductive biology, particularly the pollination system.
- 4) Assessment of the occurrence of plants as a function of vegetation density.
- 5) Quantification of the degree of herbivory.

CHAPTER II

MATERIALS AND METHODS

STUDY LOCATIONS

I conducted the majority of my field work on Penstemon lemhiensis at the Big Hole National Battlefield, Montana during the summer of 1982. Additional data were collected from populations at Argenta, Lemhi Pass, and Badger Pass, Montana and Colson Creek and Bannack Pass, Idaho (Fig. 1). At these six locations, the elevation ranges from 1158 m at Colson Creek to 2250 m at Bannack Pass. Exposures are generally south-facing; only Colson Creek has a west northwest exposure. Slope varies from nearly level ground at Bannack Pass to 60% at Colson Creek. A summary of elevation, slope, and aspect for each location appears in Table 1. Sagebrush (Artemesia tridentata), and the grasses Agropyron spicatum and Festuca idahoensis comprise the dominant vegetation at these locations.

At the Battlefield, Penstemon lemhiensis occurs on benchland below the Visitor's Center and on the sagebrush steppe on the southeast face of Battle Mountain (Fig. 2). The bench is at an elevation of 2073 m and faces southwest. The slope varies from nearly level ground to 30%. The sagebrush steppe is divided into two distinct areas by a ravine. The elevation north of the ravine ranges from 1881

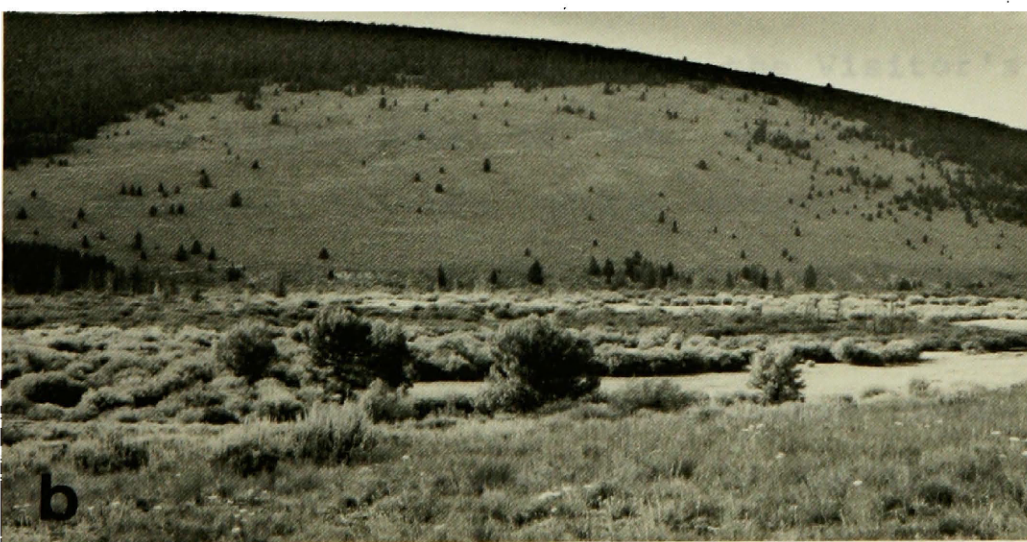
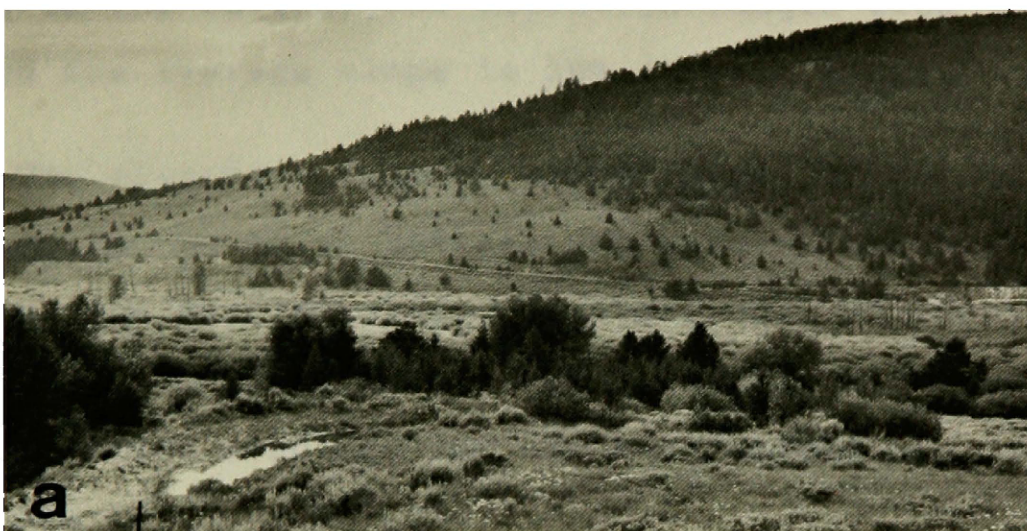
Table 1
 Summary of Elevation, Slope and Aspect
 for Six Penstemon lemhiensis Locations

<u>LOCATION</u>	<u>ELEVATION (meters)</u>	<u>SLOPE (percent)</u>	<u>ASPECT</u>
Argenta, MT Sec. 15 T6S R11W	2004 m	38%	SSE
Badger Pass, MT Sec. 16 T7S R11W	2202 m	20-45%	SSE
Battlefield, MT Sec. 24 T2S R17W			
Northern sagebrush slope	1899 m	40%	SSE
Southern sagebrush slope	2058 m	30%	SSE
Roadcut	1892 m	30-45%	SSE
Bench	2073 m	0-30%	SSW
Lemhi Pass, MT Sec. 15 T10S R15W	1981 m	0-40%	S
Bannack Pass, ID T15S R14W	2250 m	0-15%	SE
Colson Creek, ID Sec. 13 T23N R15E	1158 m	60%	WNW

Figure 2

The Battlefield, MT Penstemon lemhiensis Location

- a. Southern Sagebrush Slope in the background;
area below Visitor's Center in the foreground
- b. Northern Sagebrush Slope in the background



to 2103 m, and the average slope is 40%. On the steppe south of the ravine, the elevation ranges from 1885 to 2016 m, and the average slope is 30% (Pierce 1982).

The climatic regime within the range of Penstemon lemhiensis is quite severe. At Wisdom, Montana (nine miles east of the Battlefield), there are only 30 frost free days per year (Cordell 1971). Mean monthly air temperature and precipitation readings for the Battlefield are included in Appendix 1.

PHYSICAL AND BIOTIC CHARACTERISTICS OF THE HABITAT

Each of the six Penstemon lemhiensis locations was characterized with regard to elevation, aspect, and slope. Soil temperature and moisture data were collected at the Battlefield on 2 July, 1 August, and 28 August 1982. Measurements were made adjacent to a P. lemhiensis individual on the bench area below the Visitor's Center, on the sagebrush slope south of the ravine, and along the roadcut adjacent to the slope (Figure 3). Temperature readings were obtained using a mercury thermometer that was shaded from the sun during all readings. The thermometer was inserted in the soil and remained there until no temperature change was apparent. At the three sites, data were collected from four cm below the soil surface and near the rooting depth of P. lemhiensis at 20 cm. Tins

Figure 3

Occurrence of Penstemon lemhiensis at the Battlefield, MT and Experimental Sites

- a. Southern Sagebrush Slope (Steppe)
- b. Roadcut Above Old Park to Park Highway
- c. Northern Sagebrush Slope (Steppe)
- d. Below Visitor's Center (Bench)



Forest Boundary

● Sites for Vegetation Sampling

▲ Sites for Soil Moisture and Temperature Sampling

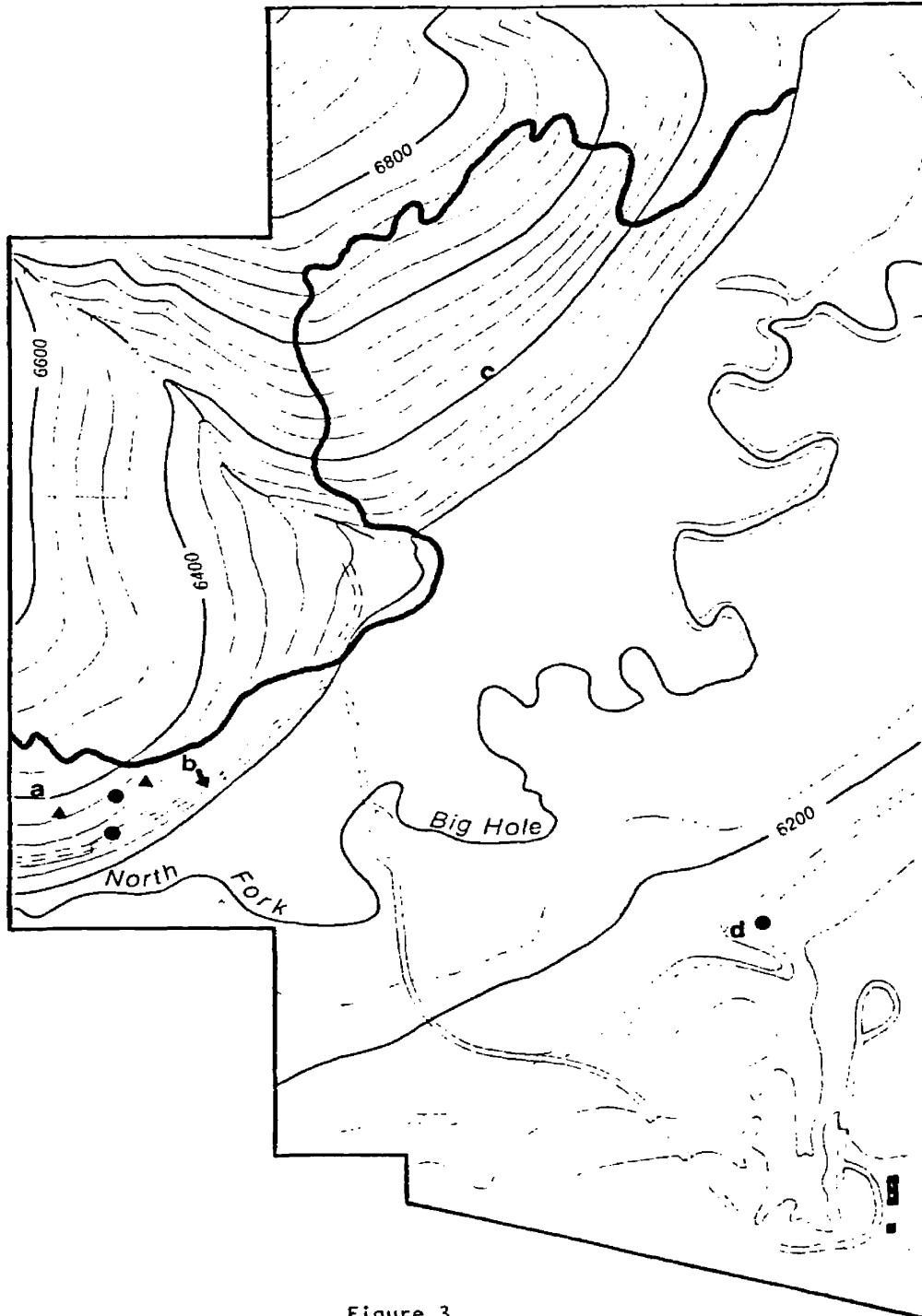


Figure 3

containing soil samples were taped to prevent water loss and weighed to the nearest one-tenth of a gram. The samples were then dehydrated for 24 hours in an oven at 105 C and reweighed. Qualitative field assessments as described by Ball (1976) were made of the following soil characteristics at the three soil sampling sites at the Battlefield: soil texture, organic matter, moisture, porosity, and stone content.

The dominant vegetation and the associated angiosperm species that were conspicuous at the time of sampling were identified at all Penstemon lemhiensis locations. At the Battlefield, quantitative data on associated species were collected from one-meter-square quadrats. A description of the sampling technique used is included in the section on competitive abilities.

POPULATION-DESCRIPTIONS

Data on the approximate number of Penstemon lemhiensis individuals at each of the six locations were collected. Exact counts were made below the Visitor's Center and on the southern sagebrush slope at the Battlefield, Colson Creek, and Bannack Pass. The number of individuals, a value for sociability-dispersion, and nearest neighbor distances for P. lemhiensis plants were recorded in 21 one-meter-square plots at the Battlefield. The Braun-Blanquet

Sociability-Dispersion index (Mueller-Dombois and Ellenberg 1974) was used:

- 5 = Growing in large, almost pure stands
- 4 = Growing in small colonies or forming larger carpets
- 3 = Forming small patches or cushions
- 2 = Forming small clumps or dense groups
- 1 = Growing solitarily

The general population structure of P. lemhiensis was determined in 1983 by assigning plants to one of the following categories:

- 1) Seedlings and immature plants = plants with small rosettes; no inflorescences produced
- 2) Mature plants = old inflorescence stalks present and/or blooming inflorescences present
- 3) Senescent plants = numerous yellowing or reddish rosette leaves; no inflorescences produced

Ninety-three plants were censused at Argenta, 23 at Badger Pass, 14 at the Battlefield, and 30 at Lemhi Pass.

REPRODUCTIVE BIOLOGY

Several aspects of the reproductive biology of Penstemon lemhiensis were studied at the Battlefield during the period from 12 June to 13 September 1982. These aspects

included phenology, seed germination, pollination biology, and the breeding system. The phenology of flowering, seed and fruit development, fruit dehiscence, and seed dispersal was observed at the Battlefield; differences in phenology at the other locations were noted when possible.

Seed germination was studied in the lab. Seeds were collected from the Battlefield, Argenta, and Badger Pass. Two-hundred and fifty seeds were soaked overnight, sterilized using a 6% Clorox solution and placed on moist filter paper using sterile technique. Seeds were then divided among five treatments: 1) room temperature, 2) scarified, 3) cold treated in a refrigerator for a minimum of two weeks, 4) scarified and cold-treated, and 5) treated with a 10⁻⁶ N solution of gibberellic acid (GA₃).

The pollination biology of Penstemon lemhiensis was studied primarily at the Battlefield during 1982. I noted the behavior of the insects under various weather conditions and at different times of the day throughout the blooming period from 29 June to 31 July. On 6 July 1982, I also observed pollinators at Argenta, Lemhi Pass, and Badger Pass. In 1983, I observed pollinators at Lemhi Pass, Argenta, Badger Pass, and the Battlefield from 23-26 July. Representatives of each insect species found visiting the flowers were collected. Dr. George Bohart at the USDA Bee Biology Lab, Utah State University identified the insects.


The breeding system of Penstemon lemhiensis was investigated using plants below the Visitor's Center, on the southern sagebrush slope, and along the roadcut at the Battlefield (Fig. 3). The study included experiments to determine 1) the level of seed set under natural conditions; 2) the amount of cross-pollination; 3) the amount of self-pollination; and 4) seed production due to apomixis. Five treatments were designed to address the preceding questions: A--Control: flowers were not experimentally manipulated. B--Emasculated: anthers from each flower were removed with forceps before the anthers dehisced. C--Cross-pollinated: pollen was obtained from the anthers of one plant and placed on the stigmas of another plant. D--Self-pollinated: pollinator exclosures made of mosquito netting were placed over inflorescences prior to anthesis. As the flowers opened, the bag was removed, and the flowers were pollinated with pollen from the same plant. The bag was then replaced over the stalk and the procedure repeated until all flowers were hand-pollinated. E--Stigmas removed: stigmas and a portion of the style were removed from each flower as it opened.

Each of these five treatments originally contained 12 inflorescence stalks; some of these inflorescences were eaten by deer during the course of the experiments. In Treatments A, C, and D, some inflorescences were collected

Figure 3

Occurrence of Penstemon lemhiensis at the Battlefield, MT and Experimental Sites

- a. Southern Sagebrush Slope (Steppe)
- b. Roadcut Above Old Park to Park Highway
- c. Northern Sagebrush Slope (Steppe)
- d. Below Visitor's Center (Bench)

 Forest Boundary

● Sites for Vegetation Sampling

▲ Sites for Soil Moisture and Temperature Sampling

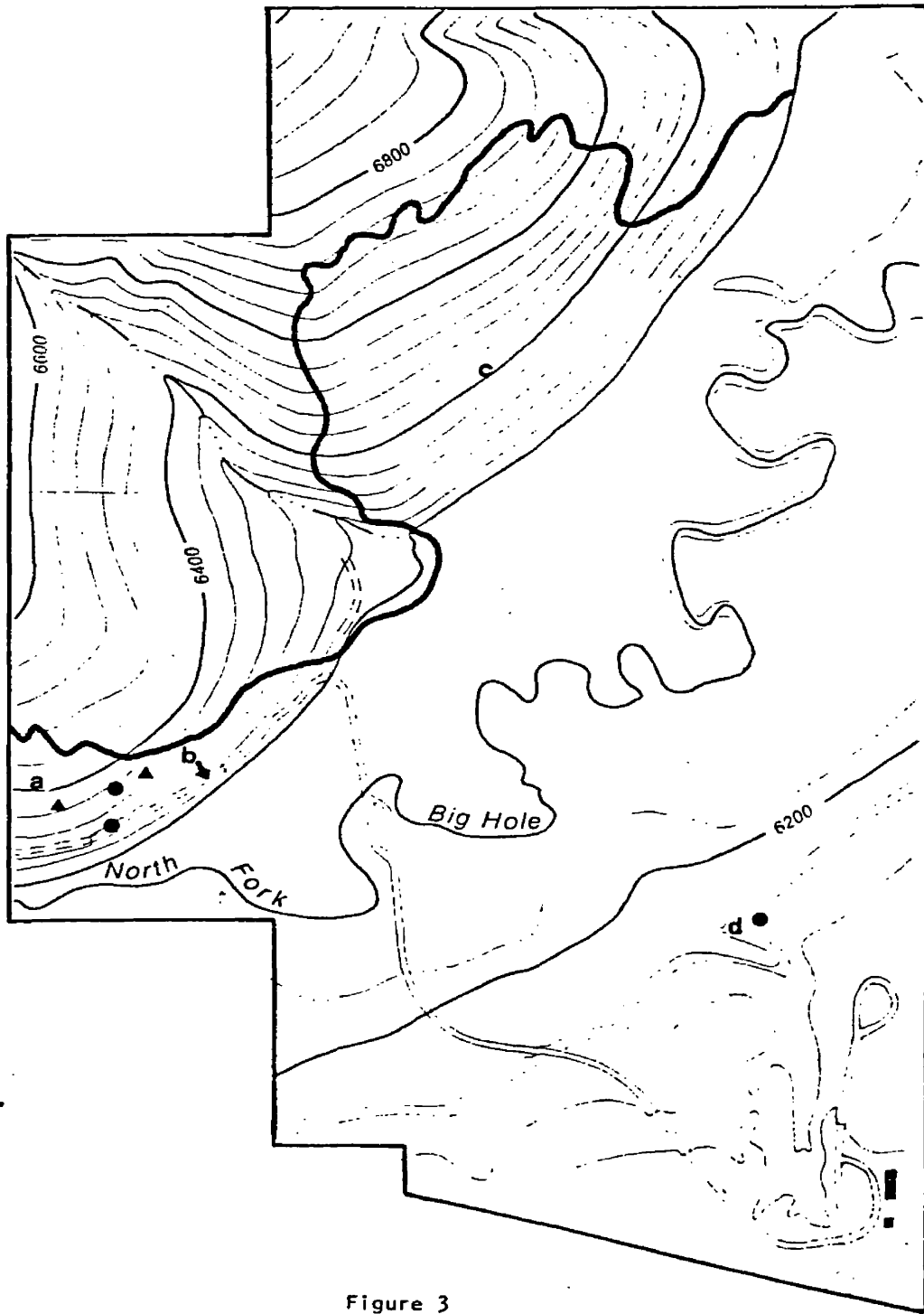


Figure 3

as soon as ovule development could be detected and the remainder were collected when the seeds were mature and fruits just beginning to dehisce. The first collection was made to assess the level of pollination, and the second was made to test for the possibility that some seed abortion occurs after fertilization. In Treatment B, all stalks were collected when ovule development could be detected because nearly half of them had been eaten by this time. In Treatment E, all stalks were collected when the seeds were mature because little seed development could be detected prior to this time. Seed set percentages were calculated by dividing the number of seeds produced per flower by the approximate number of ovules in each flower. A mean value for the number of ovules per flower was based on the number of ovules counted in six flowers.

COMPETITIVE ABILITIES

On the sagebrush steppe at the Battlefield, and at all locations, there are areas in which Penstemon lemhiensis is abundant and adjacent areas where no plants are found. The most conspicuous difference between areas with P. lemhiensis and areas without it appears to be the density of vegetation. Areas with P. lemhiensis seem to be less heavily vegetated than areas in which the species is absent. To quantify this apparent difference, percent vegetation cover was compared in areas with P. lemhiensis and in areas

without it. Two general sampling sites on the steppe were chosen: one below a large stand of Douglas firs and one near the breeding system study plants (Fig. 3). At both sites, a 30-meter transect was placed through the center of density of the P. lemhiensis plants, and ten plots were sampled. Below the Douglas firs, the transect ran east-west down the slope (east southeast-facing with 30% slope). In the breeding system study area, the transect ran north-south across the slope (east-facing with 50% slope). In each three meter segment of the transect, the P. lemhiensis individual closest to and on the appropriate side of the tape was located, and a one-meter-square plot frame was placed with the plant as the plot center.

It was necessary to use a different sampling technique in adjacent areas without Penstemon lemhiensis plants. Because there were no P. lemhiensis individuals to use as plot centers, the plots were simply placed next to the transect tape. Plots were read every five meters and on alternate sides of the tape. Two transects were run to approximate the width of the adjacent area with P. lemhiensis plants that was sampled. For the plots below the Douglas firs, the two transects (10 plots) ran east-west downhill and began where no P. lemhiensis plants were found (south southeast-facing with 30% slope). In the breeding system study area, the two transects (10 plots) ran

north-south across the slope and also began where there were no P. lemhiensis plants (east-facing with 25% slope). A total of 20 plots were sampled in areas containing P. lemhiensis and 20 plots in areas thought not to contain it. One P. lemhiensis individual was found in the heavily vegetated area sampled.

In the 40 plots sampled, cover values were assigned to conspicuous angiosperm species, as well as the litter and bare ground. All grass species were considered in a single category. The Braun-Blanquet Cover-Abundance Scale (Mueller-Dombois and Ellenberg 1974) was used to obtain these values:

5 = Any number, with cover greater than 75%

4 = Any number, with 50-75% cover

3 = Any number, with 25-50% cover

2 = Any number, with 5-25% cover

1 = Numerous, but less than 5% cover,

or scattered with up to 5% cover

HERBIVORY

Penstemon lemhiensis sustained herbivory damage in the form of browsed inflorescences and insect damage to ovules, flowers, and rosettes at all six locations visited. Quantitative data on herbivory were collected at the Battlefield, Bannack Pass, and Argenta. At the Battlefield,

the percentage of browsed P. lemhiensis stalks was compared with the percentage of browsed Tragopogon dubius, Potentilla gracilis, and Gilia aggregata stalks on 17 July 1982. On 28 July 1982, the percentage of browsed stalks, aborted stalks, and insect damaged stalks was calculated at Bannack Pass. At Argenta, the number of browsed stalks was recorded on 27 August 1982.

GENETIC VARIATION

An attempt was made to compare genetic variation in Penstemon lemhiensis and P. cyaneus populations, but no results were obtained. Starch gel electrophoresis was used to detect genetic variation of proteins in ungerminated and germinated seeds using techniques described by Allendorf et al. (1977). No enzymatic activity was apparent in ungerminated seeds, and germinated seeds were active at only one locus. I had little success in germinating my limited supply of seeds, so no attempts were made to modify the electrophoretic techniques.

CHAPTER III

RESULTS AND DISCUSSION

PHYSICAL AND BIOTIC CHARACTERISTICS OF THE HABITAT

Physical Setting

At the six locations visited, Penstemon lemhiensis most frequently occupies steep sagebrush hillsides with predominantly south-facing exposures. However, these do not appear to be strict slope and exposure requirements. At four of the six locations, the slope ranges from 30-60%, but P. lemhiensis occurs on nearly level ground below the Visitor's Center at the Battlefield, in some areas near Lemhi Pass, and at Bannack Pass. Five of the six locations have predominantly southern exposures; only Colson Creek has a west-northwest exposure (Table 1).

Penstemon lemhiensis grows in generally dry, sandy soils at all locations. Rocks are often conspicuous on the soil surface. More detailed field analyses of soil characteristics were carried out at the Battlefield, and this information is presented in Table 2. The soil on the southern sagebrush slope and the roadcut below it is a loamy sand, while the bench soil is a silty clay high in organic matter. The clayey soil should have a higher soil moisture capacity than the loamy soil, and this is reflected in the soil moisture data obtained from the three sampling sites at

Table 1

Summary of Elevation, Slope and Aspect
for Six Penstemon lemhiensis Locations

<u>LOCATION</u>	<u>ELEVATION (meters)</u>	<u>SLOPE (percent)</u>	<u>ASPECT</u>
Argenta, MT Sec. 15 T6S R11W	2004 m	38%	SSE
Badger Pass, MT Sec. 16 T7S R11W	2202 m	20-45%	SSE
Battlefield, MT Sec. 24 T2S R17W			
Northern sagebrush slope	1899 m	40%	SSE
Southern sagebrush slope	2058 m	30%	SSE
Roadcut	1892 m	30-45%	SSE
Bench	2073 m	0-30%	SSW
Lemhi Pass, MT Sec. 15 T10S R15W	1981 m	0-40%	S
Bannack Pass, ID T15S R14W	2250 m	0-15%	SE
Colson Creek, ID Sec. 13 T23N R15E	1158 m	60%	WNW

Table 2

Soil Features of Three Penstemon lemhiensis Sites
at the Battlefield, MT as Determined by Field Analysis

<u>FEATURE</u>	<u>SITE</u>		
	SOUTHERN SAGEBRUSH SLOPE	ROADCUT	BENCH
Texture Class	Loamy sand at both depths	Loamy sand at both depths	Silty clay at 20 cm; less clay at 4 cm
Organic Matter Content	Moderate at both depths	Low at both depths	High at both depths
Stone Content	Occasional	Frequent	Occasional
Porosity	Good	Good	Poor
Moisture	Dry	Dry	Moist

the Battlefield (Table 3). At a depth of 20 cm (the approximate rooting depth of P. lemhiensis), the soil moisture content increases from 7% (roadcut--sandy soil) to 22% (bench--clay soil) for 2 July 1982. This pattern is apparent in the 1 August and 28 August readings also. In general, soil moisture percentages decrease, and soil temperatures increase from early July to late August. Exceptions to this include a decrease in temperature from 22 to 19 C on the roadcut and no change from 17 C on both the southern steppe and the bench from 1 August to 28 August at the 20 cm depth.

Although the soil moisture content is higher in the clay soil, the additional water is not necessarily available to plants because water molecules bind more tenaciously to fine clay particles than they do to coarser sand particles. Soil temperature also affects the ability of plants to extract water from the soil; plants can extract water more easily from warm soils than from cold ones (Larcher, 1980). Soil temperatures were highest on the roadcut (sandiest, driest soil), lower on the sagebrush steppe, and lowest on the bench (clayey, moist soil). However, the greatest differences in soil temperature were found near the soil surface (4 cm below), rather than near the rooting zone of P. lemhiensis (20 cm below) (Table 3). More precise analyses of soil texture, moisture, and temperature are

Table 3
Soil Moisture and Temperature Data
from Three Penstemon lemhiensis Sites at the Battlefield

	SOUTHERN STEPPE		ROADCUT		BENCH	
	SMC	ST	SMC	ST	SMC	ST
7/2/82						
4 cm	0.12	22°	0.04	27°	0.42	17°
20 cm	0.16	16°	0.07	20°	0.22	15°
8/1/82						
4 cm	0.05	26°	0.05	31°	0.17	19°
20 cm	0.12	17°	0.07	22°	0.14	17°
8/28/82						
4 cm	0.05	27°	0.02	32°	0.08	21°
20 cm	0.06	17°	0.04	19°	0.07	17°

SMC (soil moisture content): Percent water in soil (fresh-dry wt./
dry wt.)

ST (soil temperature): Degrees centigrade

needed to demonstrate if there are appreciable differences among these three P. lemhiensis sites at the Battlefield.

Vegetation

Artemesia tridentata (sagebrush) is the dominant shrub at the six locations, and Festuca idahoensis also occurs at all locations. The dominant grass species vary from location to location. At the Battlefield, Agropyron spicatum is the most abundant grass; Festuca idahoensis, Stipa spp., and Koeleria cristata occur less frequently. Agropyron spicatum and Festuca idahoensis are the dominant grass species at Colson Creek, Lemhi Pass, and Bannack Pass. Appendix 1 lists these dominant species and other conspicuous herbaceous species associated with Penstemon lemhiensis. Grasses, Artemesia tridentata, Hieracium cynoglossoides, Solidago spp., and Lithospermum ruderale were the species with the highest cover values in 40 one-meter-square plots sampled at the Battlefield (Table 4). Frasera albicaulis, Eriogonum umbellatum, and Achillea millefolium occurred in over one-half of the plots that also contained P. lemhiensis (Table 4). Although the presence of F. albicaulis appears to be most closely correlated with the occurrence of P. lemhiensis (occurring in over 75% of the plots containing P. lemhiensis), F. albicaulis was not found at any of the other five P. lemhiensis locations. Additionally, F. albicaulis occurs frequently in areas

Table 4

Mean Cover Values for Associated Species at the Battlefield

<u>SPECIES</u>	<u>% OCCURRENCE IN P. LEMHIENSIS PLOTS</u>	<u>MEAN COVER VALUE</u>
Grasses		
<u>Agropyron spicatum</u>)	100%	3.3
<u>Festuca idahoensis</u>)		
<u>Koeleria cristata</u>)		
<u>Stipa spp.</u>)		
<u>Artemesia tridentata</u>	100%	2.7
<u>Hieracium cynoglossoides</u>	43%	1.4
<u>Solidago spp.</u>	33%	1.3
<u>Lithospermum ruderales</u>	38%	1.1
<u>Frasera albicaulis</u>	76%	1.1
<u>Aster spp.</u>	23%	1.1
<u>Eriophyllum lanatum</u>	38%	1.1
<u>Eriogonum umbellatum</u>	76%	1.1
<u>Penstemon lemhiensis</u>	100%	1.1
<u>Achillea millefolium</u>	48%	1.0
<u>Geranium viscosissimum</u>	24%	1.0
<u>Lupinus sp.</u>	10%	1.0
<u>Viola sp.</u>	--	1.0
<u>Gilia aggregata</u>	14%	1.0
<u>Antennaria</u>	29%	1.0
<u>Potentilla sp.</u>	--	1.0
<u>Arenaria sp.</u>	--	1.0
<u>Balsamorhiza sagittata</u>	5%	1.0
<u>Collinsia parviflora</u>	5%	1.0
<u>Castilleja cusickii</u>	29%	1.0

where P. lemhiensis does not grow at the Battlefield.

Plants occurring at all six locations include Eriogonum umbellatum and Lupinus spp.; Rosa woodsii, Achillea millefolium, Castilleja spp., Antennaria sp., and Aster spp. occur at four or more of the locations (Appendix 2). In addition to its occurrence at all locations, Eriogonum umbellatum was found in 52% of the plots sampled that contained P. lemhiensis at the Battlefield. Aside from Artemesia tridentata, the grasses, and Frasera albicaulis, E. umbellatum occurs in more P. lemhiensis plots than any other species. The constancy of E. umbellatum in the plots sampled and its occurrence at all locations indicate that E. umbellatum may be a species consistently associated with P. lemhiensis.

POPULATION DESCRIPTIONS

Population size

There is wide variation in the size of the Penstemon lemhiensis populations at the six locations visited. The populations are quite small at Colson Creek and Bannack Pass, with 21 and 61 individuals respectively. Along a 5.5 km stretch of road at Lemhi Pass, P. lemhiensis occurs in four distinct areas; these areas are separated by at least 0.3 km and 4 km at the most. Approximately 150 plants were found near Lemhi Pass. At Argenta, some 300 plants were in

bloom. At the Battlefield, there were 342 plants of all ages on the southern steppe, 105 plants on the roadcut adjacent to the steppe, and approximately 40 plants on the bench below the Visitor's Center. There are also scattered plants in sagebrush areas below the old Park to Park Highway and a sizable population on the northern steppe. No attempt was made to count the exact number of individuals, but the plants appear to be more widely dispersed over a larger area on the northern steppe (about ten hectares) than on the southern steppe (about five hectares). Table 5 summarizes information on the number of individuals at each of the six locations. All of these data are approximate; there are hundreds of hectares of sagebrush hillsides surrounding each location that were not searched systematically. At each location, I surveyed hillsides immediately adjacent to the reported populations with no success. My most extensive survey was near the Battlefield; while searching the south face of Battle Mountain, two hillsides across Highway 43 to the south of the Battlefield, and two hillsides to the north of the Battlefield, I found no additional plants. I also searched several hillsides north and west of the Argenta population with no success. However, an additional population was found in that vicinity in 1983 (Pierce, pers. comm.).

Table 5
Summary of Population Size
at Six Penstemon lemhiensis Locations

Argenta, MT (<2.5 hectares)

Sagebrush slope: ~300 plants in bloom

Badger Pass, MT (<2.5 hectares)

Sagebrush slope: ~50 plants

Disturbed area: ~30 plants

Battlefield, MT

Southern sagebrush slope: 342 plants

Northern sagebrush slope: unknown

Roadcut: 105 plants

Below Visitor's Center: ~40 plants

Lemhi Pass, MT

Sagebrush slopes, level areas, roadcuts: ~150 plants

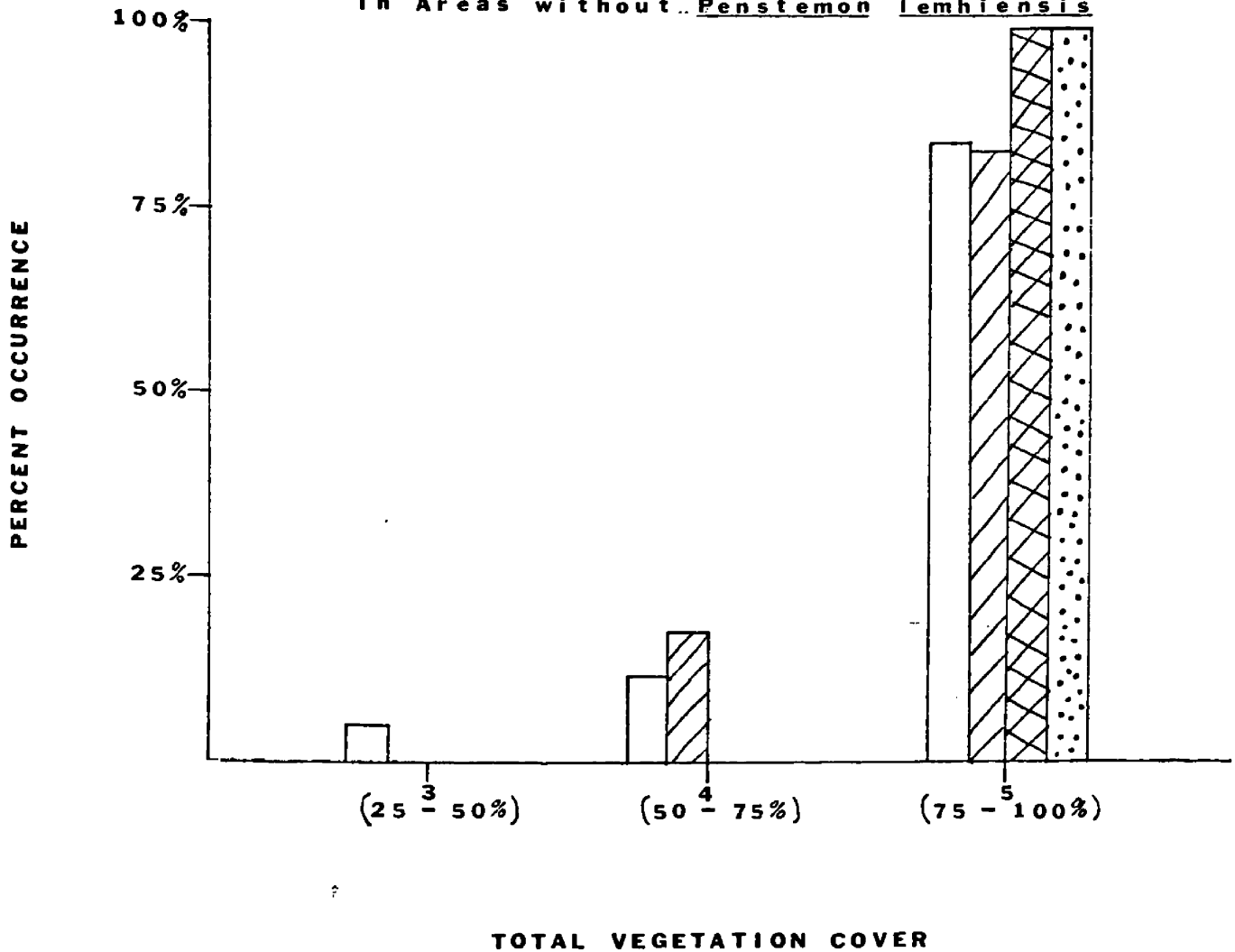
Bannack Pass, ID

Level area: 61 plants - 38 reproductive; 23 vegetative

Colson Creek, ID

Sagebrush slope: 21 plants - 5 reproductive; 16 vegetative

Proportionate Occurrence of Three Species as a Function of Vegetation Density in Areas without Penstemon lemhiensis



TOTAL VEGETATION COVER

All Plots Sampled

Eriogonum umbellatum

Frasera albicaulis

Hieracium cynoglossoides



Proportionate Occurrence:

$$\frac{\text{\# of plots with species present at given cover}}{\text{\# of total plots with species present}}$$

Based on the total number of individuals, the Battlefield and Argenta may have the most viable populations among those visited; there are several hundred individuals at each location. The plants at Bannack Pass, Colson Creek, and Badger Pass may represent single, relatively small populations at each location; most individuals are in close proximity to one another, and there is a consequent likelihood of gene exchange. In contrast, the several distinct Penstemon lemhiensis sites at the Battlefield and at Lemhi Pass may be sufficiently separated to permit only minimal gene flow and may represent several populations at each of the locations. This also may be the case in the Argenta area, depending on the extent of populations there. Should a disturbance occur at the Battlefield or Lemhi Pass, it is likely that some individuals would not be threatened. In contrast, P. lemhiensis individuals at Bannack Pass, Colson Creek, and Badger Pass are restricted to comparatively small areas (less than 2.5 hectares each), and there seems to be only one central population at each location. A disturbance could potentially eliminate all individuals because they are in close proximity, and they are likely to share similar genes. There would be less opportunity for individuals to be physically isolated from the disturbance or to possess unique gene combinations enabling them to tolerate the disturbance more successfully.

Population Structure

Data collected on the number of Penstemon lemhiensis individuals, their sociability-dispersion, and nearest neighbor distances within one-meter-square quadrats provide some information on the general population structure of P. lemhiensis at the Battlefield. General age class estimates made at Argenta, Badger Pass, the Battlefield, and Lemhi Pass also aid in describing population structure.

The mean number of individuals was 2.3 per plot in the 21 plots sampled. The mean sociability-dispersion value for Penstemon lemhiensis in the plots was 1.25. The associated species Frasera albicaulis, Achillea millefolium, and Eriogonum umbellatum had mean sociability-dispersion values of 1.04, 1.04, and 1.76 respectively. Frasera albicaulis and A. millefolium were usually growing solitarily in an unclumped fashion, while P. lemhiensis and E. umbellatum individuals tended to grow more closely together. Table 6 summarizes the mean sociability-dispersion values for species occurring in over one-fourth of the plots sampled.

The mean distance from the Penstemon lemhiensis individual sampled to the next closest angiosperm individual in the plots was 3.85 cm. In 70% of the plots, more than one P. lemhiensis individual was found. The mean distance between P. lemhiensis individuals in the plot was 20.32 cm.

Table 6

Mean Sociability-Dispersion Values for Species Occurring
in Over One-Fourth of 40 Plots at the Battlefield

<u>SPECIES (# of plots of occurrence)</u>	<u>MEAN SOCIABILITY- DISPERSION VALUE</u>
Grasses (40) <u>Agropyron spicatum</u> , <u>Festuca</u>) <u>Idahoensis</u> , <u>Koeleria cristata</u> ,) <u>Stipa</u> spp.)	2.30
<u>Eriogonum umbellatum</u> (17)	1.76
<u>Hieracium cynoglossoides</u> (18)	1.50
<u>Penstemon lemhiensis</u> (21)	1.24
<u>Lithospermum ruderales</u> (14)	1.08
<u>Achillea millefolium</u> (24)	1.04
<u>Frasera albicaulis</u> (26)	1.04
<u>Artemesia tridentata</u> (40)	1.00
<u>Geranium viscosissimum</u> (15)	1.00

A summary of data on the distribution of P. lemhiensis within the plots appears in Table 7.

Table 7

Distribution of Penstemon lemhiensis within
One-Meter-Square Plots

Mean # individuals/plot: 2.3

Mean sociability-dispersion value: 1.24

Mean distance to nearest angiosperm: 3.9 cm

Mean distance to nearest conspecific: 20.3 cm

Penstemon lemhiensis populations appear to be rather uniform in their age class composition at the four locations surveyed. Seedlings and immature plants comprise from 30-35% of the plants found, mature plants from 40-60%, and senescent plants from 10-25% (Table 8). Seedling percentages are most likely to be underestimates because of the greater likelihood of overlooking the smallest plants and difficulty in distinguishing between large individual rosettes and possible resprouts or seedlings adjacent to mature plants.

Table 8

General Population Structure of Penstemon lemhiensis
at Four Locations

<u>SITE</u> (# of plants censused)	<u>PERCENTAGE OF PLANTS IN EACH GENERAL AGE CLASS</u>		
	SEEDLINGS & IMMATURE	MATURE	SENESCENT
Argenta, MT (93 plants)	30%	60%	10%
Badger Pass, MT (23 plants)	35%	40%	25%
Battlefield, MT (14 plants)	30%	50%	20%
Lemhi Pass, MT (30 plants)	30%	60%	10%

REPRODUCTIVE BIOLOGY

Phenology

In 1982, Penstemon lemhiensis flower buds began to develop by 12 June, and plants were in bloom by 27 June. In general, anthesis of flowers on inflorescences is acropetal; all flowers in an inflorescence opened within three to five days. The flowers are protandrous; anthers dehisced approximately two days before the stigma appeared to be receptive. I judged a stigma to be receptive when the style curved downward toward the anthers, and the stigma became enlarged and sticky. Prior to these events, the style and stigma were straight and uniform in size and texture.

On 13 September, all inflorescences observed had mature fruits. However, even in the dehisced capsules, many seeds still remained in the capsules in mid-September. The seeds have no hairs or conspicuous wings that might aid in long-distance dispersal. I found no evidence that capsules are consumed as food and the seeds thus dispersed. I believe that the majority of the seeds merely fall from dehisced capsules. Once released, it is doubtful that the seeds are transported any great distance from the parent plant.

In 1983, most inflorescences at Argenta, Badger Pass, and Lemhi Pass had dropped their flowers, and fruits were developing during 23-26 July. At the Battlefield, most flowers had dropped, but no developing fruits were seen. Observations made in 1982 and 1983 indicate that the sexual reproductive period at higher elevations is somewhat shorter than at lower elevations. Figure 4 depicts the reproductive phenology for P. lemhiensis during 1982.

Seed Germination

It is unknown when the seeds of Penstemon lemhiensis germinate after dispersal. Judging from the severity of the winter and considering that dispersal is so late in the growing season, I suspect that germination occurs in the spring. Evidence from seed germination experiments in the lab also suggests that P. lemhiensis germinates in the spring. Of the five treatments, only seeds that were cold-treated or treated with gibberellic acid germinated. Gibberellic acid is known to substitute for a cold treatment when germinating seeds (Salisbury and Ross 1978). In each of these treatments, only about 4% of the seeds germinated after approximately two weeks; most seeds did not germinate at all. It is likely that seeds of P. lemhiensis also require a cold treatment prior to germination in the field.

Observed Reproductive Phenology
of Penstemon lemhiensis

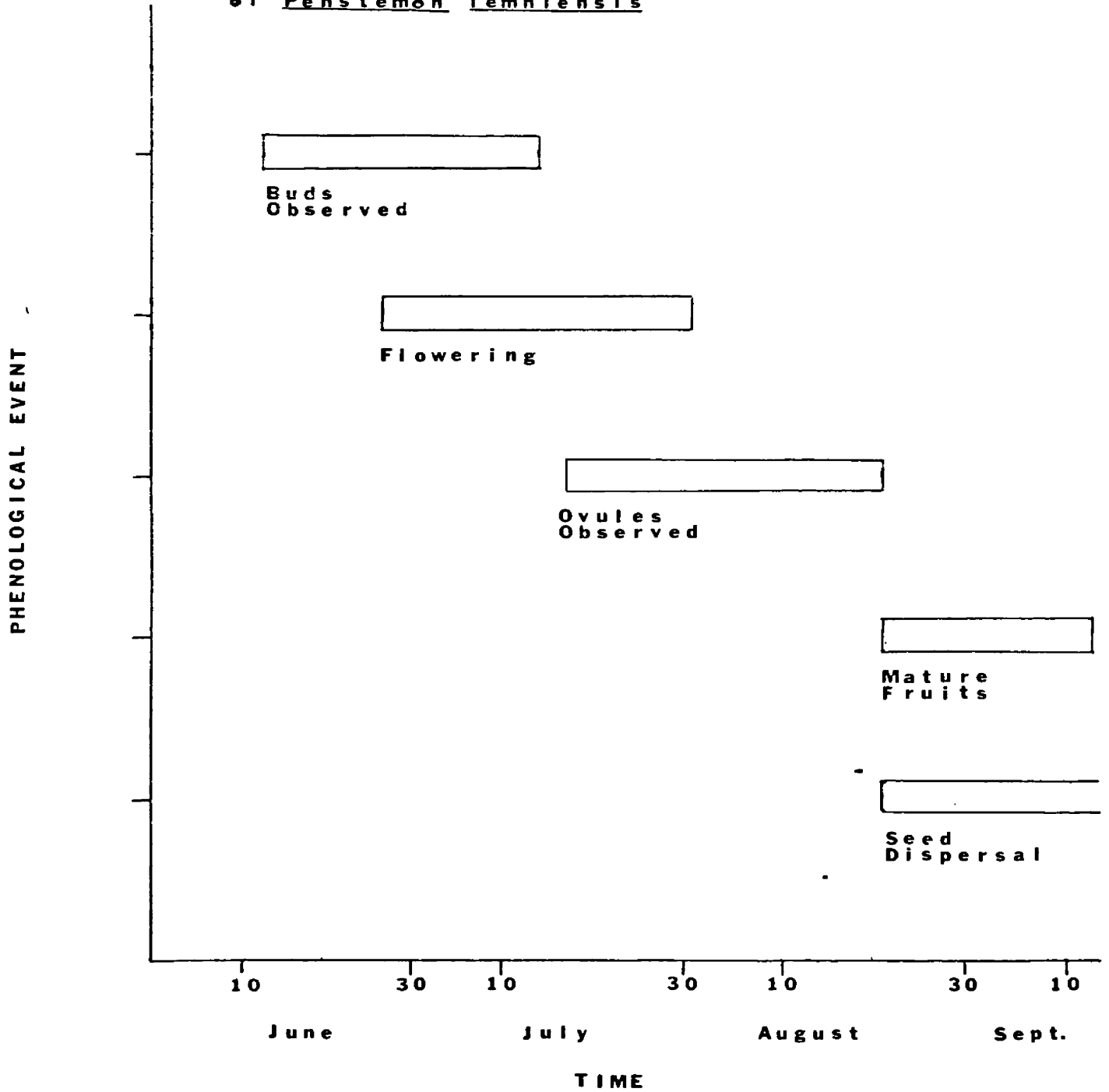


Figure 5

Insect Species Collected on Penstemon lemhiensis

- | | | |
|----|--------------------------------|-------|
| a. | <u>Pseudomasaris vespoides</u> | ♂ |
| b. | <u>Pseudomasaris vespoides</u> | ♀ |
| c. | <u>Osmia brevis</u> | ♀ + ♂ |
| d. | <u>Lasioglossum trizonatus</u> | ♀ |
| e. | <u>Lasioglossum trizonatus</u> | ♂ |
| f. | <u>Osmia bruneri</u> | ♀ |
| g. | <u>Osmia bucephala</u> | ♀ |
| h. | <u>Bombus centralis</u> | ♀ |
| i. | <u>Anthophora ursina</u> | ♀ |
| j. | <u>Bombus appositus</u> | ♀ |
| k. | <u>Bombvlius</u> sp. | |
| l. | Anthomyiidae, Fucellinae | |
| m. | <u>Melanostoma</u> sp. | |
| n. | <u>Dialictus</u> sp. | ♀ |
| o. | <u>Hyaleus modestus</u> | ♀ |

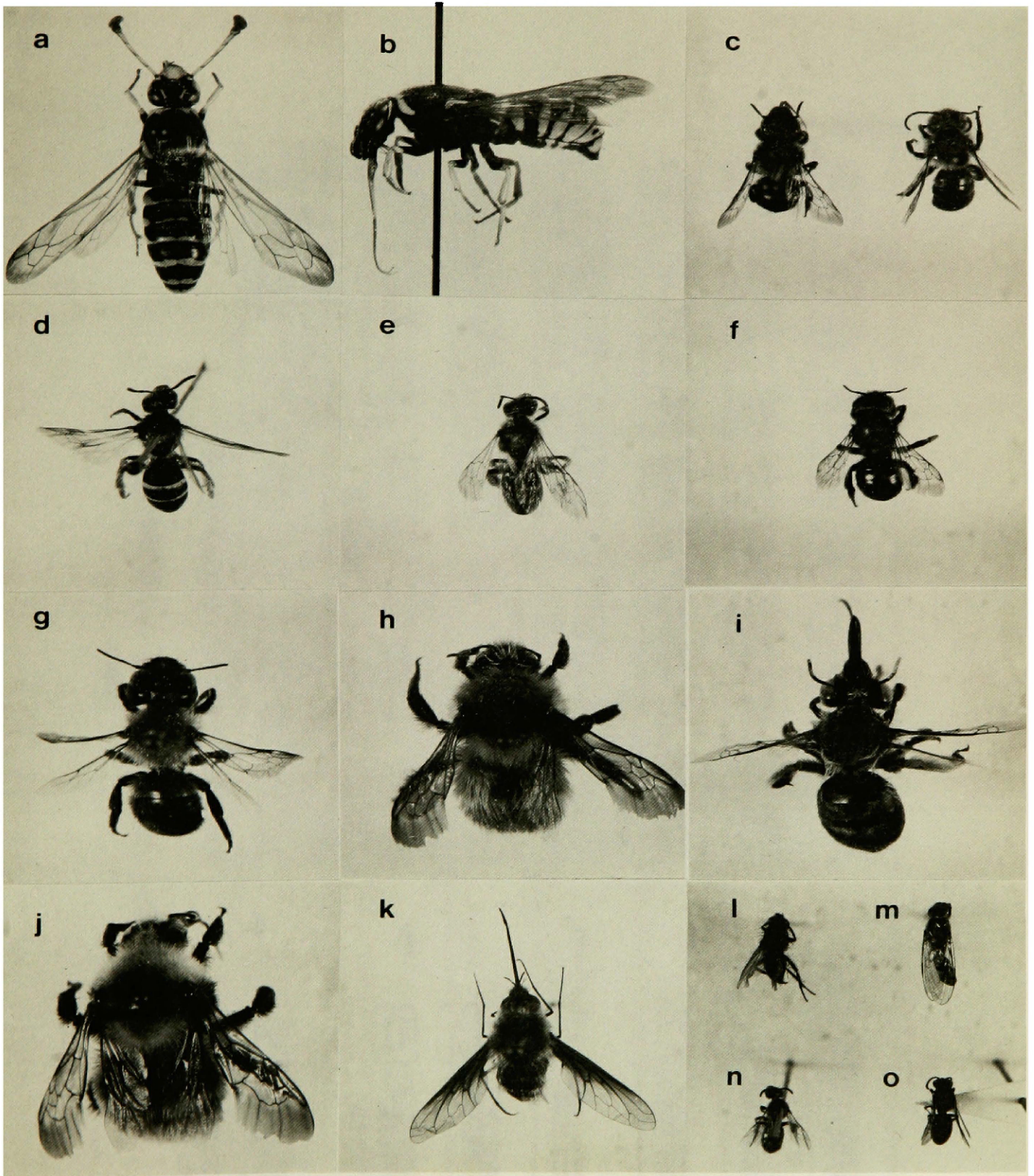


Table 9
Insect Visitors and Pollinators on Penstemon lemhiensis

INSECT SPECIES
(Family, Subfamily)

OCCURRENCE AND BEHAVIOR ON PENSTEMON LEMHIENSIS

<u>Pseudomasaris vespoides</u> Cresson (Vespididae, Masarinae)	Pollinator. Body length ♂ 24 mm; ♀ 17 mm. Width: 4 mm. Proboscis length: 10 mm. ♀s and ♂s abundant at Argenta, Badger Pass and Battlefield; only visitor at Lemhi Pass (1982). Only visitor at Argenta, Badger Pass and Lemhi Pass (1983). Pollen-collecting, acropetal visits, consistent contact with stamens and stigmas. Seen only on <u>P. lemhiensis</u> .
<u>Osmia brevis</u> Cresson (Megachilidae, Megachilinae)	Pollinator. Body length: 9 mm. Width: 3 mm. Proboscis length: 5 mm. ♀s and ♂s abundant at Battlefield and Argenta (1982). Nectar-seeking, consistent contact with stamens and stigmas.
<u>Lasioglossum trizonatus</u> Cresson (Halictidae, Halictinae)	Possible pollinator. Body length: 10 mm. Width: 3 mm. ♀s and ♂s occasional at Battlefield and Argenta (1982). Sporadic contact with stamens and stigmas. Pollen thievery observed once.
<u>Osmia bruneri</u> Cockerell (Megachilidae, Megachilinae)	Unlikely important pollinator. Body length: 10 mm. Width: 3 mm. Proboscis length: 5 mm. Abundant on 1st day of pollinator activity at Battlefield, but seen only once during remainder of blooming period (1982). Contact with stamens and stigmas.
<u>Osmia bucephala</u> Cresson (Megachilidae, Megachilinae)	Unlikely important pollinator. Body length: 15 mm. Width: 5 mm. Proboscis length: 6 mm. Seen only once at Battlefield (1982). Contact with stamens and stigmas.
<u>Bombus centralis</u> Cresson (Apidae, Apinae)	Unlikely important pollinator. Body length: 15 mm. Width: 8 mm. Proboscis length: 6 mm. Seen only once at Battlefield (1982). Contact with stamens and stigmas.
<u>Anthophora ursina</u> Cresson (Apidae, Anthophorinae)	Unlikely important pollinator. Body length: 15 mm. Width: 5 mm. Proboscis length: 10 mm. Seen only once at Battlefield (1982). Contact with stamens and stigmas.

Table 9 (continued)

<u>INSECT SPECIES</u> (Family, Subfamily)	<u>OCCURRENCE AND BEHAVIOR ON PENSTEMON LEMHIENSIS</u>
<u>Bombus appositus</u> Cresson (Apidae, Apinae)	Visitor. Body length: 20 mm. Width: 10 mm. Proboscis length: 14 mm. Seen only once at Battlefield (1982). Too large to contact stamens and stigmas.
<u>Melanostoma</u> sp. (Syrphidae)	Visitor. Body length: 9 mm. Width: 2 mm. Occasional at Battlefield (1982). Entered corollas, but no contact with stamens and stigmas.
(Anthomyiidae, Fucillinae)	Visitor. Body length: 9 mm. Width: 2 mm. Occasional at Battlefield (1982). Entered corollas, but no contact with stamens and stigmas.
<u>Hyaleus modestus</u> Say (Halictidae, Halictinae)	Visitor. Body length: 6 mm. Width: 1 mm. Occasional at Battlefield (1982). Entered corollas, but no contact with stamens and stigmas.
<u>Dialictus</u> sp. (Halictidae, Halictinae)	Visitor. Body length: 6 mm. Width: 1 mm. Occasional at Battlefield (1982). Entered corollas; often seen eating pollen; no contact with stigmas.
<u>Bombylius</u> sp. (Bombyliidae)	Visitor. Body length: 10 mm. Width: 4 mm. Proboscis length: 7 mm. Abundant at all sites (1982). Hovered, never entered corolla.

Figure 6

Pseudomasaris vespoides visiting a Penstemon lemhiensis flower



the pollen from their bodies. One specimen, collected at Lemhi Pass, had a ball of pollen attached to hairs near its mouthparts. Penstemon lemhiensis appears to provide P. vespoidea with a significant source of pollen, and pollen is probably the primary attractant for the wasp. During my observations, the wasp never extended its proboscis (Figure 5b) into the corolla for nectar-feeding. I was unable to extract a measureable amount of nectar from the flowers using a capillary tube. Further evidence that pollen is important for nutrition is that I never saw the wasps completely entering flowers in which the anthers had been removed for Treatment B of the breeding system study. They partially entered emasculated flowers, but then backed out and did not fully enter any flowers until they encountered ones that were not emasculated.

As the Pseudomasaris wasps collected pollen, some was deposited nototribically and was then transferred to the stigmas of Penstemon lemhiensis. The wasp visited flowers acropetally, moving from the lowest to the highest flowers on an inflorescence. During the blooming period of P. lemhiensis, I never encountered P. vespoidea visiting flowers other than those of P. lemhiensis.

Osmia brevis was another frequent visitor to Penstemon lemhiensis. Both males and females were abundant throughout the blooming period at the Battlefield and were also observed at Argenta. The insects appeared to be nectar-seeking, and were seen with their probosces extended into the throat of the corollas. Upon entering a flower, O. brevis often went deep into the corolla and remained there for several seconds. In the process, pollen on their heads and backs was placed on the stigmas. In general, an individual visited several flowers per inflorescence and several inflorescences in the area before flying to another plant species or out of view. On foraging trips to P. lemhiensis, O. brevis also visited co-blooming species such as Frasera albicaulis and Achillea millefolium.

Less frequent visitors to Penstemon lemhiensis included Lasioglossum trizonatus (Fig. 5,d and e), Anthophora ursina (Fig. 5i), Bombus centralis (Fig. 5h), O. bucephala (Figure 5g), and O. bruneri (Fig. 5f). Lasioglossum trizonatus (males and females) was observed occasionally at the Battlefield and at Argenta. On some visits to P. lemhiensis, pollen was deposited on the head and back of this Halictid, and contact was then made with the stigmas. On other visits, L. trizonatus did not appear to contact the stigmas, and its only contact with the stamens was to consume pollen. Anthophora ursina, B. centralis, and O.

bucephala each were seen once on P. lemhiensis. All of these insects were dusted with pollen nototribically and made contact with the stigmas. However, because each insect species was observed only once during the blooming period, they probably did not contribute significantly to the pollination of P. lemhiensis. Osmia bruneri, a species very similar in size and shape to O. brevis, was abundant on the first day of pollinator activity on P. lemhiensis at the Battlefield. Aside from that first day, I saw only one other O. bruneri individual, on 10 July 1982.

Insect species that did not appear to effect pollination in Penstemon lemhiensis on any of their visits included one that did not enter the corollas and five that did enter but did not place pollen on the stigmas. All six species were infrequent visitors to P. lemhiensis. A large bumblebee Bombus appositus (Fig. 5j), attempted to enter the corolla, but only could partially fit its head into the flower; no contact with the stigma was made. In contrast, an Anthomyiid fly and Melanostoma sp. (Dipterans) and the Hymenopterans Dialictus sp. and Hyaleus modestus (Fig. 5, l-o) are very small; they did not contact the stigmas in their movements in the flowers. Only Dialictus sp. contacted the stamens, and this was while perched on the anthers consuming pollen. Flies in the genus Bombylius (Fig. 5k) hovered at the mouths of corollas with their

probosces extended into flowers. Their visits were restricted to one or two flowers per inflorescence and they usually moved to flowers other than P. lemhiensis on their next visit.

Based on the preceding evidence, I believe that Pseudomasaris vespoides and Osmia brevis are the most important pollinators of those insects collected. The morphology and behavior of both species enables them to place pollen on the stigmas consistently. Additionally, both species visited numerous flowers and inflorescences in succession. If P. vespoides is as constant to Penstemon lemhiensis as my observations indicate, the wasp may be an especially important pollinator. A high percentage of the pollen brought to the stigmas would be from P. lemhiensis; very little foreign pollen would be deposited that might compete for space on the stigmas. Furthermore, very little P. lemhiensis pollen would be deposited wastefully on other plant species.

Breeding system

Data obtained from breeding system experiments at the Battlefield suggest that Penstemon lemhiensis is an obligate out-crosser capable of producing a large crop of seeds. The number of seeds actually produced may be somewhat limited by the level of pollination. Agamospermy contributes little,

if any, to the reproductive effort. The breeding system data are summarized in Table 10.

In Treatment A (control), 18.55% of the ovules were initiated as seeds. Control stalks collected in September when the seeds were mature yielded 17.80% seed set. The difference between the values for seed initiation and seed maturation are not statistically significant using a Chi-squared test. Once seed development begins in P. lemhiensis there is apparently little seed abortion.

Although the seed set value for Penstemon lemhiensis is relatively high, the number of seeds actually produced may be somewhat pollinator-limited. The value of 29.58% seeds initiated in Treatment C (cross-pollinated by hand) is significantly higher than the value of 18.55% in Treatment A (control). The percentage of seeds actually matured in Treatment C dropped to 22.51%, again significantly higher than the value of 17.80% seeds matured in the control. The decrease in seeds matured in Treatment C suggests that an individual plant may not have the resources to mature all of the seeds initiated when the pollination level is nearly 30%.

Seed set percentages from Treatments D and B indicate that Penstemon lemhiensis is essentially an obligately cross-pollinated species. First, very few seeds were

initiated in Treatment D (self-pollinated by hand). Only 7.20% of the ovules were initiated as seeds, and the value for seeds matured dropped to 2.10% in Treatment D. Secondly, in Treatment B (emasculated), 17.29% of the ovules were initiated, not significantly lower than the value of 18.55% ovules initiated in the control treatment. Although no pollen from the same plant was available in Treatment B, the flowers still produced nearly as many seeds as in the control. Further, it is possible that some of the small difference between emasculated and control flowers resulted from lack of visitation from the wasp Pseudomasaris vespoides. As mentioned previously, the wasps I observed did not fully enter emasculated flowers.

It is doubtful that agamospermy occurs in Penstemon lemhiensis. Only 1.83% of the seeds matured in Treatment E (stigmas removed). Furthermore, these seeds may have developed after actual pollination (due to experimental error), rather than by agamospermy. I found intact stigmas in several flowers and developing fruits on Treatment E stalks. I removed all such flowers and fruits, but it is possible that I failed to remove other stigmas and subsequently maturing fruits. Although I removed stigmas every day during the blooming period, it is also likely that pollinators visited some of the flowers before I removed the stigmas.

Table 10

Breeding System Data for Penstemon lemhiensis

Ovules initiated as seeds; (Mature seeds)

	<u>TREATMENT</u>				
	<u>A</u>	<u>B</u>	<u>C*</u>	<u>D*</u>	<u>E*</u>
	<u>CONTROL</u>	<u>STAMENS REMOVED</u>	<u>HAND CROSS- POLLINATED</u>	<u>HAND SELF- POLLINATED</u>	<u>STIGMAS REMOVED</u>
% seed set	18.55%	17.29%	29.58%	7.20%	--
# seeds/ # ovules	(17.80%)	--	(22.51%)	(2.10%)	(1.83%)
\bar{x} # seeds/ flower	12 (12)	11 --	19 (14)	5 (1)	-- (1)
# seeds	5,259 (740)	1,786 --	3,783 (1,404)	1,152 (146)	-- 450
# ovules	28,350 (4,158)	10,332 --	12,789 (6,237)	16,002 (6,930)	-- 24,633
# fruits	197 (35)	60 --	124 (46)	136 (40)	-- (29)
# flowers	450 (63)	164 --	203 (99)	254 (110)	-- (391)
# inflorescences	11 (2)	7 --	6 (3)	7 (4)	-- (10)

*Difference in seed set between control and treatment statistically significant at $P < 0.05$.

The conclusions drawn here are based on breeding system data collected at one location and during one flowering season only. Levels of pollination (Treatment A) may well vary from site to site and from year to year. Variation in the location or from one season to the next should have a lesser impact on the degree of self-compatibility (Treatments C and D) and agamospermy (Treatment E). These are probably genetically determined characteristics of the species.

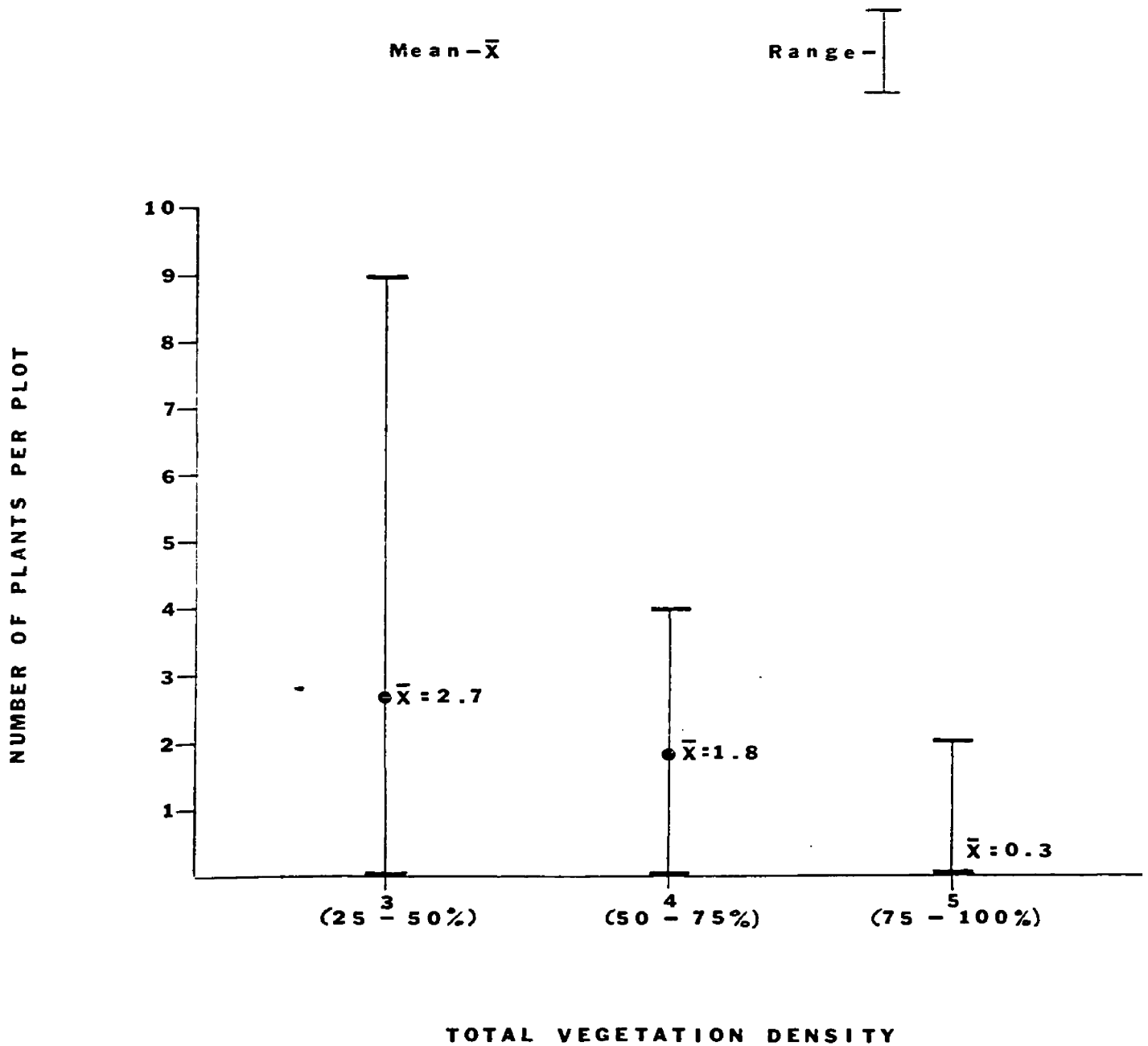
COMPETITIVE ABILITIES

Quantitative Data

Data obtained by sampling vegetation in one-meter-square plots at the Battlefield indicate that the occurrence of Penstemon lemhiensis is correlated with vegetation density. Penstemon lemhiensis grows in areas of relatively low vegetation cover (mean of 3.6 on the Braun-Blanquet Cover-Abundance Scale), but is rarely found in areas of relatively high vegetation cover (mean of 5.2). The average number of P. lemhiensis individuals per plot drops steadily from 2.7 in cover-class 3 (25-50% cover) to 0.3 in cover class 5 (75-100% cover) (Fig. 7). This pattern of sensitivity to high vegetation density is not apparent for the species associated with P. lemhiensis. Seventeen of the 19 associated species in P. lemhiensis

Figure 7

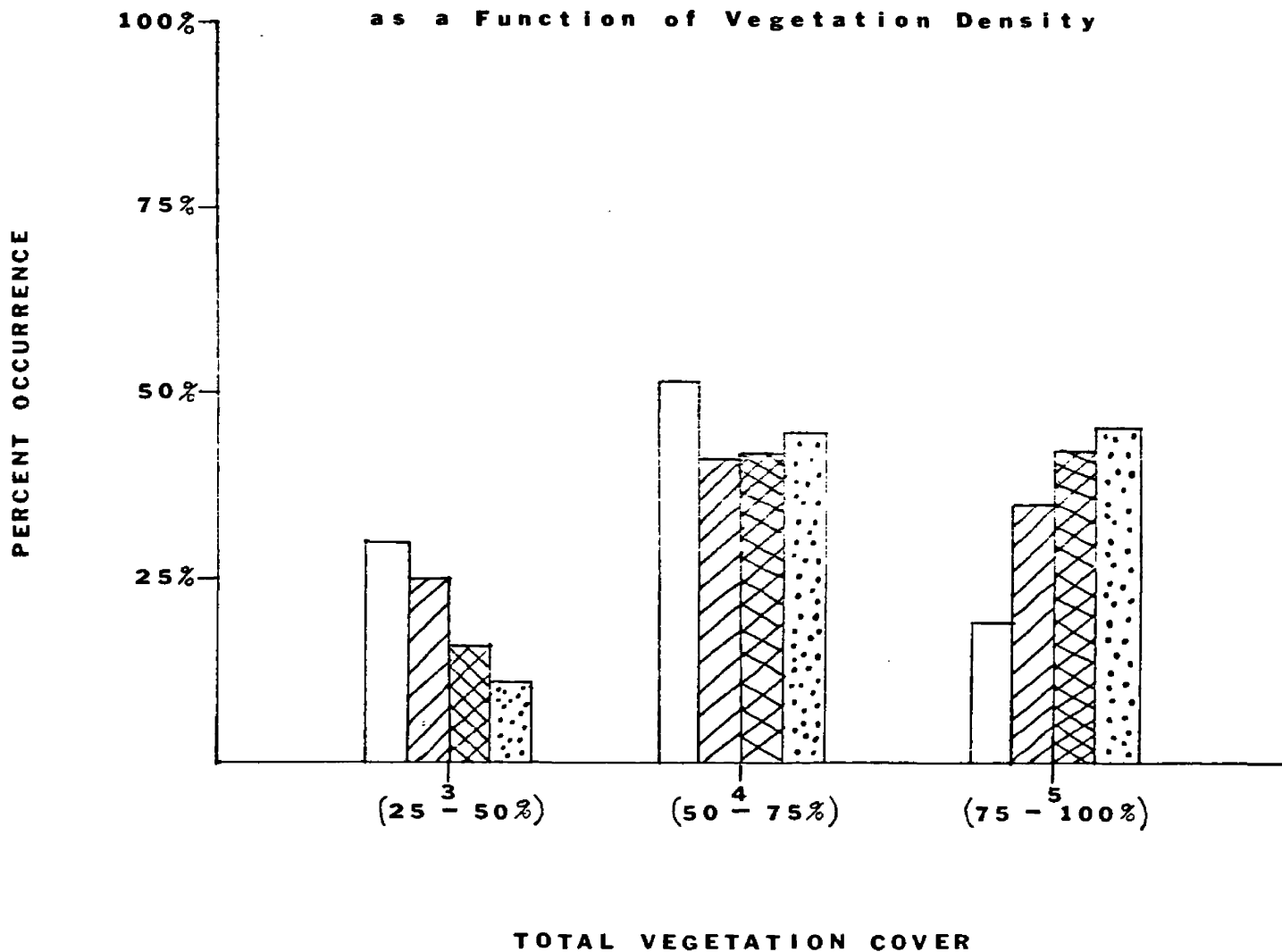
Number of Penstemon lemhiensis Plants
Per Plot as a Function of Vegetation Density



plots also were found in the heavily vegetated areas. Only Collinsia parviflora and Castilleja cusickii were restricted to areas with P. lemhiensis, and these two species were recorded only in one plot each.

The proportionate occurrence of Penstemon lemhiensis and the eight associated species occurring in the greatest number of plots as a function of total vegetation density is represented graphically in Figs. 8, 9, and 10. In Fig. 8, P. lemhiensis is compared with Frasera albicaulis, Hieracium cynoglossoides, and Eriogonum umbellatum. All four species were recorded most often in plots with a cover class of 4. Penstemon lemhiensis was recorded next most often in plots with a cover-class of 3, while the two other species occurred more frequently in plots with a cover-class of 5. Only 19% of all plots containing P. lemhiensis had a cover value of 5. The proportion of plots containing the three other species and having a cover value of 5 was higher in all cases: 42% for F. albicaulis, 45% for H. cynoglossoides, and 36% for E. umbellatum (Table 11). Figures 9 and 10 illustrate the same phenomenon, but the differences between the proportionate occurrences of the remaining five species and the proportionate occurrence of P. lemhiensis is even more apparent.

Proportionate Occurrence of Four Species
as a Function of Vegetation Density



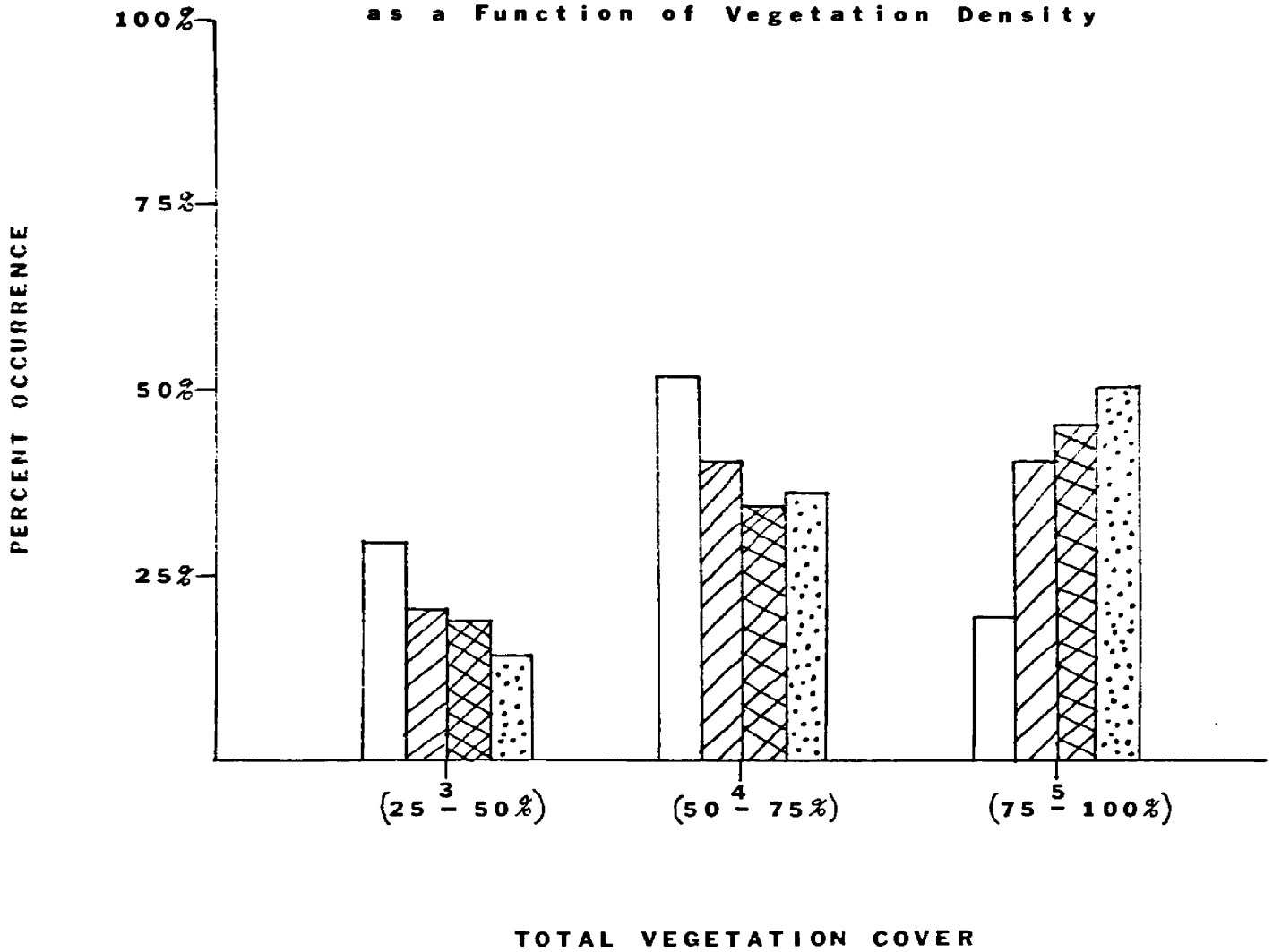
Penstemon lemhiensis
Eriogonum umbellatum
Frasera albicaulis
Hieracium cynoglossoides



Proportionate Occurrence:

$$\frac{\# \text{ of plots with species present at given cover}}{\# \text{ of total plots with species present}}$$

Proportionate Occurrence of Four Species
as a Function of Vegetation Density

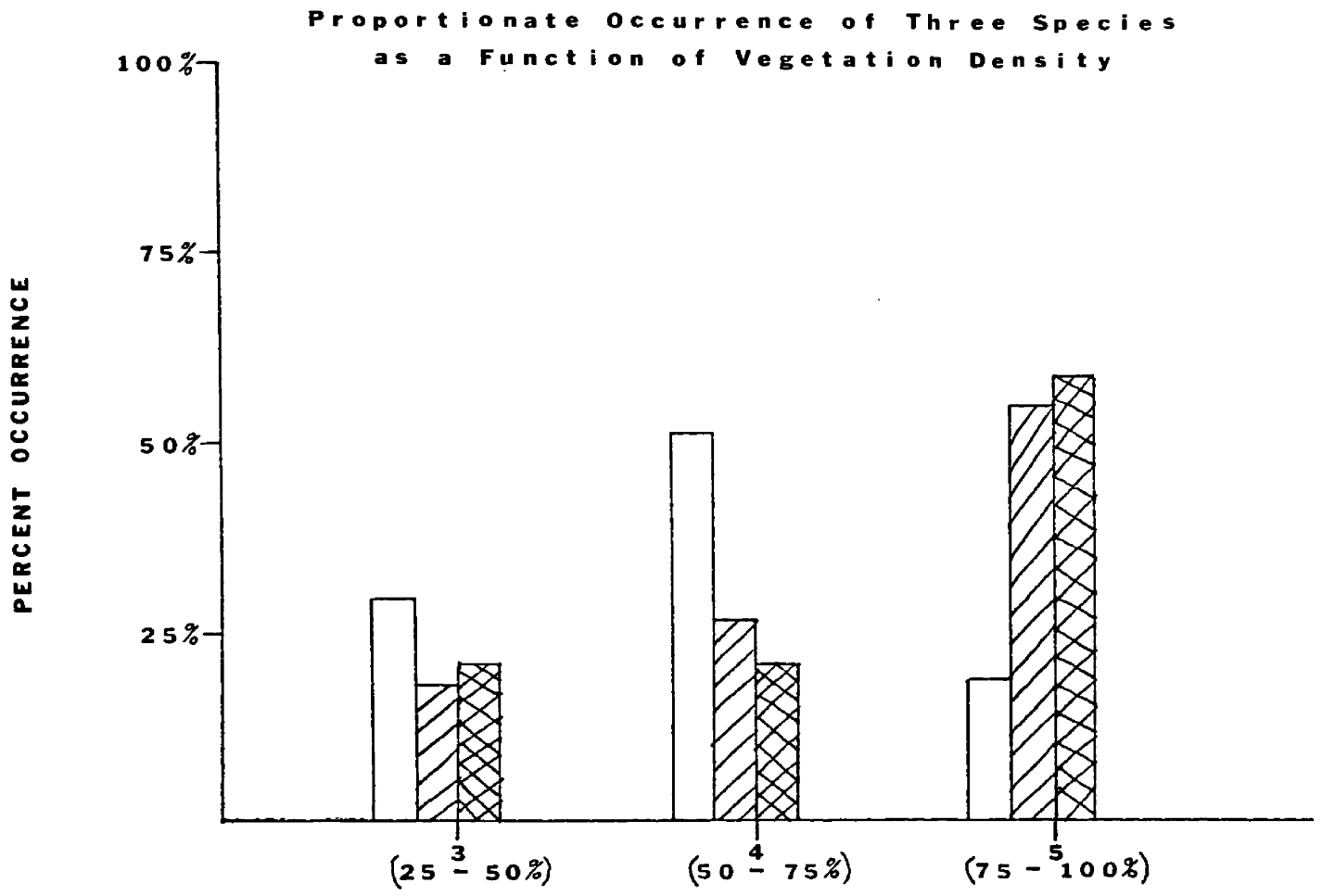


Penstemon lemhiensis
Orthocarpus tenuifolius
Achillea millefolium
Lithospermum ruderale



Proportionate Occurrence:

$$\frac{\# \text{ of plots with species present at given cover}}{\# \text{ of total plots with specie present}}$$



TOTAL VEGETATION COVER

Penstemon lemhiensis
Eriophyllum lanatum
Geranium viscosissimum



Proportionate Occurrence:

$$\frac{\text{\# of plots with species present at given cover}}{\text{\# of total plots with species present}}$$

Table 11

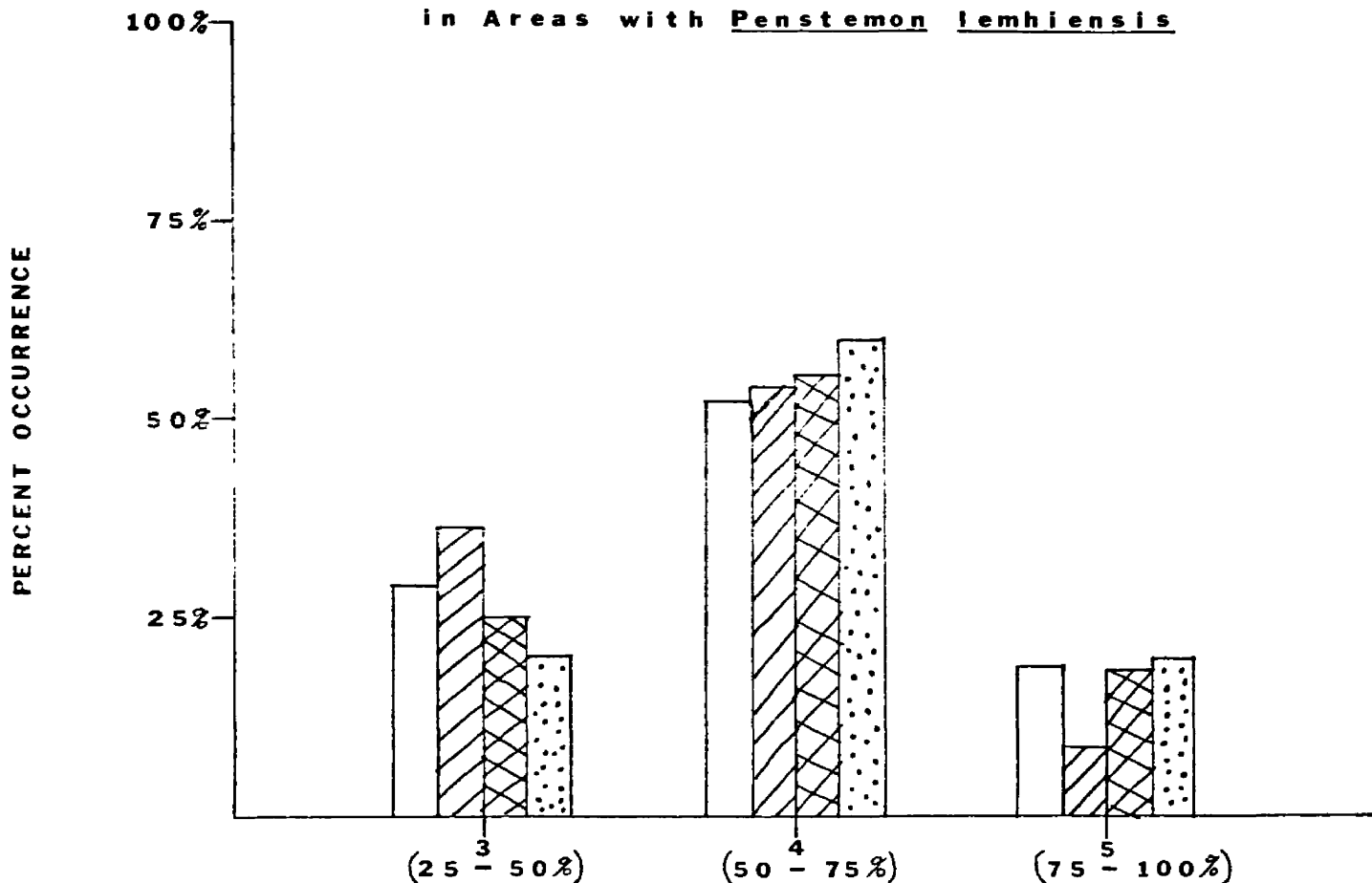
Species Occurrence as a Function of Vegetation Density
from 40 Plots Sampled at the Battlefield

SPECIES	NUMBER OF PLOTS OF OCCURRENCE (Percent Occurrence)				Total # of plots of occurrence
	3(25-50%)	4(50-75%)	5(75-95%)	> 95%	
<u>Penstemon lemhiensis</u>	6(0.29)	11(0.52)	4(0.19)	--	21
<u>Frasera albicaulis</u>	4(0.15)	11(0.42)	7(0.26)	4(0.15)	26
<u>Achillea millefolium</u>	4(0.17)	9(0.38)	4(0.16)	7(0.29)	24
<u>Hieracium cynoglossoides</u>	2(0.11)	8(0.44)	5(0.28)	3(0.17)	18
<u>Eriogonum umbellatum</u>	4(0.24)	7(0.41)	4(0.24)	2(0.12)	17
<u>Lithospermum ruderales</u>	2(0.13)	6(0.38)	3(0.19)	5(0.31)	16
<u>Geranium viscosissimum</u>	3(0.21)	3(0.21)	4(0.29)	4(0.29)	14
<u>Eriophyllum lanatum</u>	2(0.18)	3(0.27)	3(0.27)	3(0.27)	11
<u>Orthocarpus tenuifolius</u>	2(0.20)	4(0.40)	1(0.10)	3(0.30)	10
<u>Solidago spp.</u>	2(0.25)	3(0.37)	2(0.25)	1(0.13)	8
<u>Lupinus spp.</u>	1(0.17)	4(0.67)	1(0.17)	--	6
<u>Viola sp.</u>	--	--	1(0.17)	5(0.83)	6
<u>Gilia aggregata</u>	--	4(0.80)	1(0.20)	--	5
<u>Arenaria sp.</u>	--	--	--	3(1.00)	3
<u>Potentilla spp.</u>	--	--	1(0.33)	2(0.67)	3
<u>Balsamorhiza sagittata</u>	1(0.50)	1(0.50)	--	--	2
<u>Castilleja cusickii</u>	--	1(1.00)	--	--	1
<u>Collinsia parviflora</u>	1(1.00)	--	--	--	1
All plots sampled	7(0.18)	13(0.33)	12(0.30)	8(0.20)	40

To statistically test the differences in these proportionate occurrences, at least four sample classes (vegetation cover classes) are needed. By breaking cover-class 5 into two classes: 75-95% cover and greater than 95% cover (bare ground less than 5%), a Spearman Rank Correlation can be used. Although there are differences in the proportionate occurrences of the species, the ranking of all four cover classes must be different in order for the differences to be statistically significant with a sample size as small as four. All species exhibit the greatest proportionate occurrence in the 4 cover class.

Because two different sampling techniques were used to choose plots, care must be taken when interpreting the data. In areas containing Penstemon lemhiensis (generally low vegetation densities), P. lemhiensis individuals were used as plot centers to assess the species composition immediately surrounding the plants. For this reason, P. lemhiensis is represented in nearly all plots with low vegetation densities. Strictly from this non-random sample, it may not be correct to conclude that P. lemhiensis occupies areas of low vegetation density more frequently than do other species. As discussed above, however, P. lemhiensis rarely occupies areas of high vegetation density as the associated species do. For clarity, the two sampling techniques are separated in Figs. 11 and 12. In Fig. 11,

**Proportionate Occurrence of Four Species
as a Function of Vegetation Density
in Areas with Penstemon lemhiensis**



TOTAL VEGETATION COVER

All Plots Sampled	}	
<u>Penstemon lemhiensis</u>		
<u>Eriogonum umbellatum</u>		
<u>Frasera albicaulis</u>		
<u>Hieracium cynoglossoides</u>		

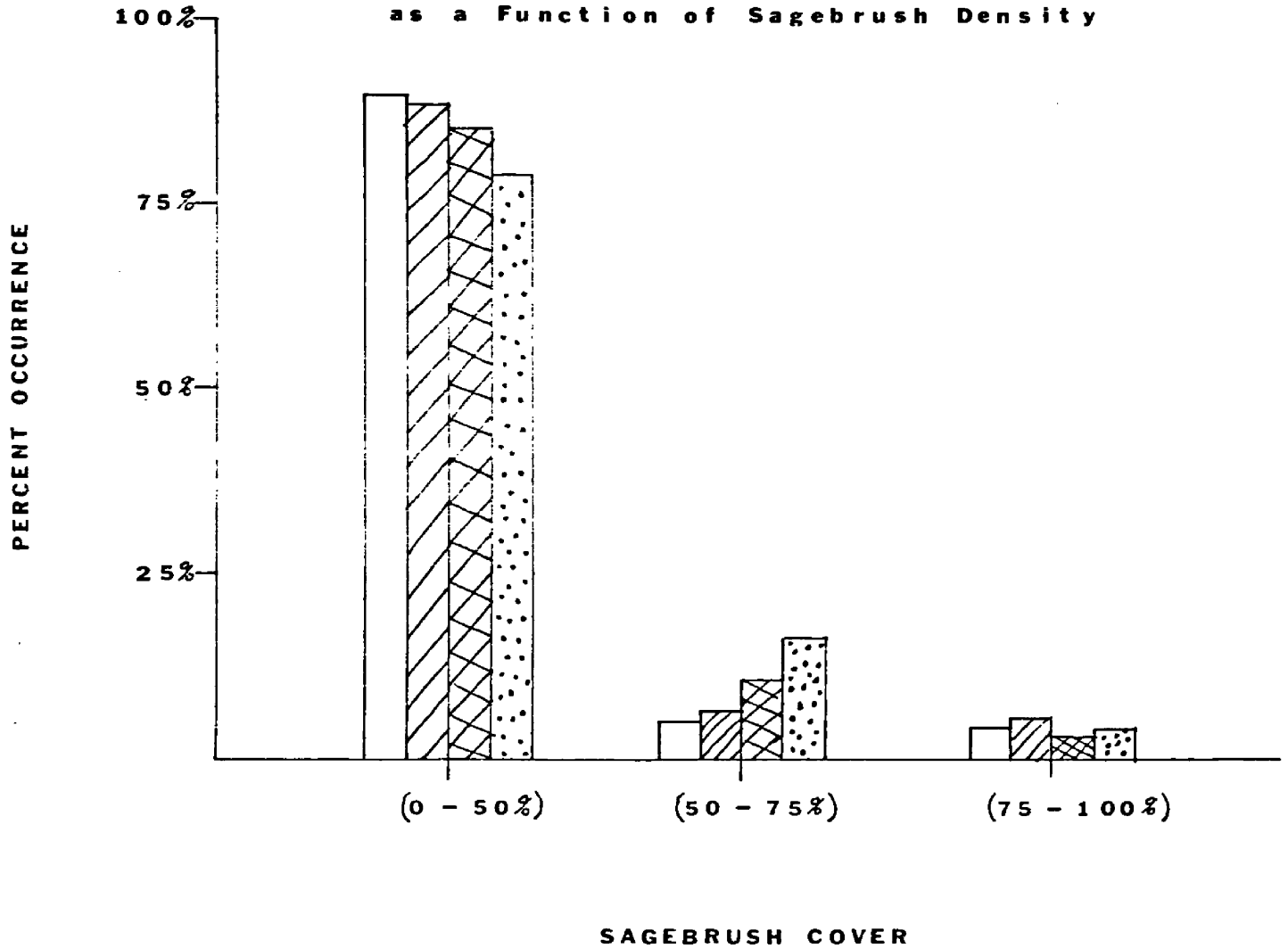
Proportionate Occurrence:

$$\frac{\# \text{ of plots with species present at given cover}}{\# \text{ of total plots with species present}}$$

the four species occur in the various cover classes approximately in proportion to the total number of plots exhibiting those cover classes. The same is true in Fig. 12, except that P. lemhiensis was not found in areas where 84% of the plots had cover values of 5. Penstemon lemhiensis was not found in any plots with greater than 95% cover. Each of the associated species discussed previously was found in two or more plots in this cover class.

The data presented thus far concern the occurrence of Penstemon lemhiensis and associated species as a function of total vegetation density. Figs. 13 and 14 illustrate comparisons of the occurrence of P. lemhiensis, Frasera albicaulis, Hieracium cynoglossoides, and Eriogonum umbellatum as a function of the density of the two dominant groups of plants: sagebrush and grasses respectively. Sagebrush (Artemesia tridentata and grasses (Agropyron spicatum, Stipa spp., Festuca idahoensis, and Koeleria cristata) are the species comprising the greatest percentage of cover, and they occurred in all 40 plots sampled. No other species occupied 50% or more of the cover in a given plot, and Hieracium cynoglossoides was the only species to occupy as much as 25-50% of a plot (one plot only). Therefore, the density of sagebrush and the grasses is likely to have the most significant effect on species' occurrences. As with total vegetation density, a smaller

Proportionate Occurrence of Four Species
as a Function of Sagebrush Density



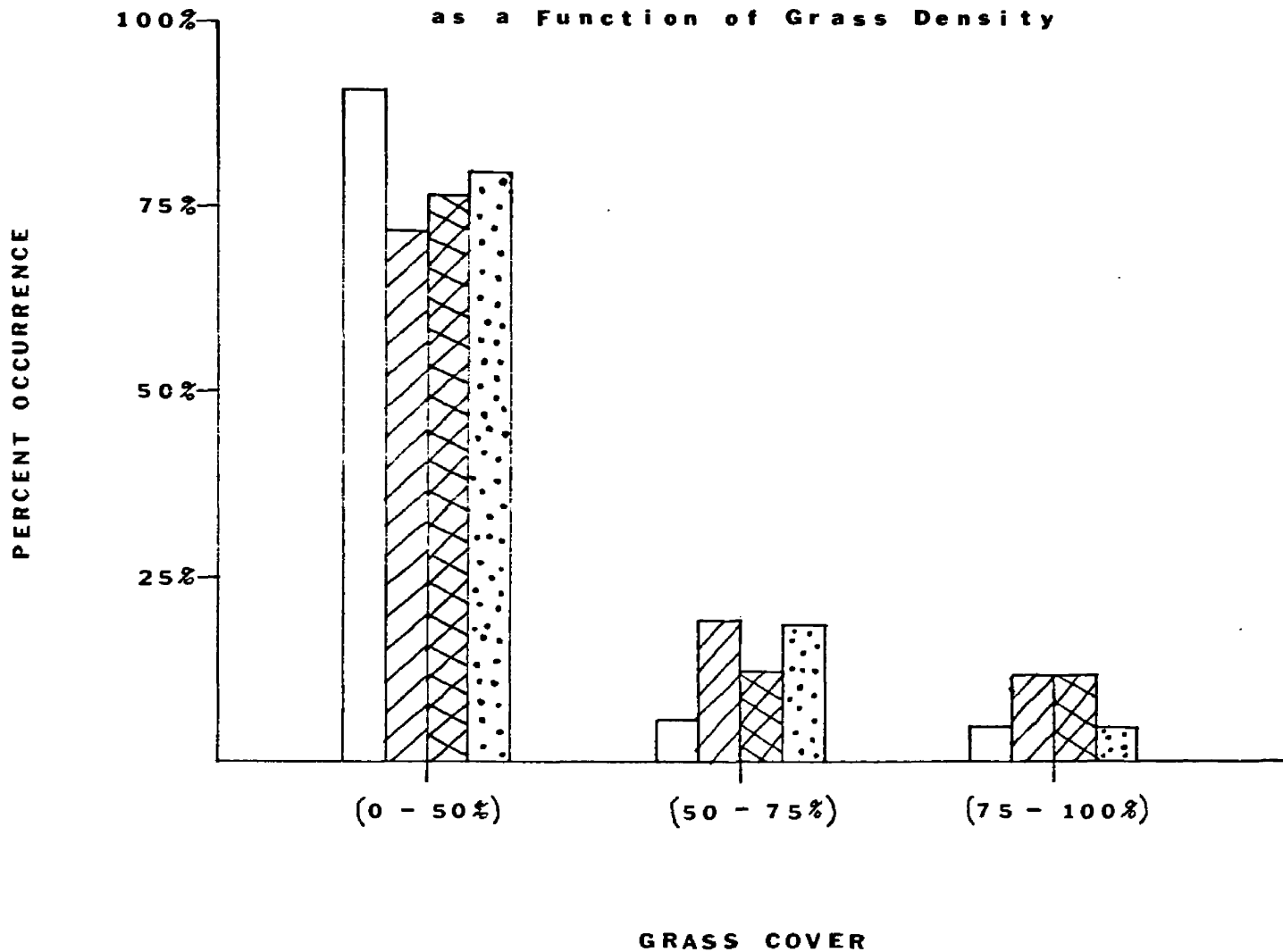
Penstemon lemhiensis
Eriogonum umbellatum
Frasera albicaulis
Hieracium cynoglossoides



Proportionate Occurrence:

$$\frac{\text{\# of plots with species present at given cover}}{\text{\# of total plots with species present}}$$

Proportionate Occurrence of Four Species
as a Function of Grass Density



Penstemon lemhiensis
Eriogonum umbellatum
Frasera albicaulis
Hieracium cynoglossoides



Proportionate Occurrence:

$$\frac{\text{\# of plots with species present at given cover}}{\text{\# of total plots with species present}}$$

proportion of P. lemhiensis individuals than other associated species were found in plots exhibiting high densities of sagebrush or grasses.

All of these data suggest that Penstemon lemhiensis may be outcompeted in areas that have high densities of vegetation (sagebrush and grasses in particular). The occurrence of the associated species does not seem to be as sensitive to high vegetation densities. It is important to emphasize that these data represent a correlation, but do not necessarily indicate causation. Other factors may be important in determining the distribution of P. lemhiensis in these areas also. For instance, soil moisture, temperature, and texture were not compared in areas with and without P. lemhiensis. Seed dispersal would definitely affect the distribution of plants as well, and there could be differential dispersal in the two areas. In addition, the slope is greater at the sites where P. lemhiensis grows than at sites where it is not found. However, I do not believe that slope itself is the critical factor. More likely, there is greater natural soil slippage on the steeper slopes, and the sagebrush and grasses are not able to dominate as they do on more gradual slopes.

Qualitative Observations

Qualitative observations lend further support to the hypothesis that Penstemon lemhiensis is particularly sensitive to competition. The species frequently colonizes areas of disturbance that are nearly devoid of other vegetation. The density of P. lemhiensis is far greater on the roadcut above the old Park to Park Highway than it is on the sagebrush slope above it; 150 plants occur on the sparsely vegetated roadcut as compared to 342 plants on the more densely vegetated sagebrush slope. The roadcut is only a few feet high, while the slope extends for several hectares (Fig. 2).

Additionally, while surveying areas north and south of the Battlefield, I never found any Penstemon lemhiensis plants. These areas are subjected to heavy cattle-grazing and are quite densely vegetated with grasses. Species such as Frasera albicaulis and Hieracium cynoglossoides are still present in the grazed areas. The absence of P. lemhiensis may be due to factors other than competition from the grasses, but I could not discern any immediately plausible factors.

A final, entirely subjective observation also may indicate that Penstemon lemhiensis is a poor competitor. I believe that the P. lemhiensis individuals below the

Visitor's Center at the Battlefield are smaller than those typically found elsewhere and perhaps are being crowded out by the lush growth of grasses. The level of reproduction was lower also; seed set was 13.1%, as compared to 19.1% for other areas at the Battlefield. Dense vegetation may have a detrimental effect on the vigor of established plants and on the reproductive capacity of mature plants.

HERBIVORY

The quantitative data I collected on herbivory suggest that Penstemon lemhiensis is susceptible to predation. At all six locations visited, inflorescence stalks were browsed or grazed. I never observed the stalks being consumed, but I believe that deer and cattle are the major herbivores. At the Battlefield, the mean height from the ground at which stalks were browsed was 36.9 cm. This height is probably too great for Columbian ground squirrels, abundant at the Battlefield, to have consumed them. Also, fresh deer footprints were found near stalks the morning after they were browsed, and deer often were seen at the three P. lemhiensis sites at the Battlefield. The height at which stalks were browsed was similar at all locations except Lemhi Pass. There the stalks were grazed within inches of the ground, and cattle rather than deer probably consumed them.

At the Battlefield, browsed inflorescences were observed below the Visitor's Center, on the sagebrush slope, and on the roadcut. I collected quantitative data on browsing along the roadcut where 23% of the inflorescences were eaten. This compares to 28%, 9%, and 3% browsed stalks for Tragopogon dubius, Potentilla gracilis, and Gilia aggregata respectively. Although 5% more T. dubius stalks were browsed, this species continued to produce inflorescences after browsing over a number of weeks. Penstemon lemhiensis produced inflorescences during a narrower blooming period, and no new stalks were produced on plants after browsing. I did not collect similar quantitative data for P. lemhiensis plants on the sagebrush slopes at the Battlefield, but browsing appeared to be less extensive on the steep hillsides than along the roadcut or below the Visitor's Center. In one area at Argenta, 90% of the stalks seen were browsed. Browsing at Argenta occurred later in the season than at the other locations visited. No bitten off stalks were observed at Argenta on 6 July, but on 27 August only five viable stalks remained. At Bannack Pass, 39% of the stalks were browsed, and 67% were consumed at Colson Creek.

I did not calculate the percentage of browsed stalks at Badger Pass or Lemhi Pass. Only five stalks remained viable at the most densely populated site along Lemhi Pass road.

Other than at the Battlefield, I did not compare the percentage of browsed Penstemon lemhiensis stalks with browsed stalks of associated species. At Bannack Pass, Potentilla glandulosa, P. gracilis, Castilleja spp., and Penstemon procerus also sustained browsing damage; only a few stalks were browsed in each of these species. Browsing occurred at the four locations visited in 1983 also: Argenta, Badger Pass, the Battlefield, and Lemhi Pass. Although browsing damage appears to be severe in P. lemhiensis, further comparisons with other species are necessary to demonstrate that P. lemhiensis is more susceptible to browsing than are other species.

In addition to browsing damage, insects also damaged the ovules and flowers of Penstemon lemhiensis. Insect larvae bored into the ovules, caterpillars were seen eating flower buds, and ants were abundant on inflorescence buds and flowers. The particular insect species causing damage were not identified; there was no evidence that the ants caused any of the damage seen. At Bannack Pass, total destruction of buds and flowers occurred in 41% of the inflorescences. An additional 11% of the stalks were damaged heavily with only a few ovules or flowers per stalk remaining viable. Also, 6% of the stalks aborted for undetermined reasons. Considering browsing, insect damage, and abortions, 95% of the stalks were destroyed at Bannack

Pass. A summary of the herbivory data appears in Table 12.

Table 12
Summary of Herbivory Data
at Four Penstemon lemhiensis locations

<u>BATTLEFIELD - DEER BROWSING</u>						
<u>SPECIES</u>	<u>TOTAL STALKS</u>	<u>UNBROWSED STALKS</u>			<u>BROWSED STALKS</u>	
<u>Penstemon lemhiensis</u>	209	162			47 (0.23)	
<u>Tragopogon dubius</u>	82	59			23 (0.28)	
<u>Potentilla gracilis</u>	82	75			7 (0.09)	
<u>Gilia aggregata</u>	74	72			2 (0.03)	

<u>BANNACK PASS - BROWSING AND INSECT DAMAGE</u>						
<u>SPECIES</u>	<u>TOTAL STALKS</u>	<u>VIABLE STALKS</u>	<u>PARTIALLY VIABLE STALKS</u>	<u>ABORTED STALKS</u>	<u>DAMAGED STALKS</u>	<u>BROWSED STALKS</u>
<u>Penstemon lemhiensis</u>	83	4(0.05)	9	5	34	31(0.39)
<u>Penstemon procerus</u>)						
<u>Potentilla spp.</u>)	Quantitative data not gathered; < 5 browsed stalks observed					
<u>Castilleja</u>)	for each species.					

<u>ARGENTA - BROWSING</u>			
<u>SPECIES</u>	<u>TOTAL STALKS</u>	<u>UNBROWSED STALKS</u>	<u>BROWSED STALKS</u>
<u>Penstemon lemhiensis</u>	51	5	46 (0.90)

<u>COLSON CREEK - BROWSING</u>			
<u>SPECIES</u>	<u>TOTAL STALKS</u>	<u>UNBROWSED STALKS</u>	<u>BROWSED STALKS</u>
<u>Penstemon lemhiensis</u>	12	4	8 (0.67)

CHAPTER IV

CONCLUSIONS AND CONSERVATION RECOMMENDATIONS

BIOLOGICAL ASPECTS OF RARITY

Rarity in Penstemon lemhiensis cannot be attributed entirely to any single ecological factor discussed here. It is likely, however, that each factor has an impact on some aspect of the occurrence of the species. In combination, these ecological factors and other factors not investigated undoubtedly play a role in determining the distribution and abundance of the species. In the following paragraphs, I will present some of the possible impacts of habitat characteristics, reproduction, competition, herbivory, genetic diversity, and evolutionary history.

Habitat

Penstemon lemhiensis is not restricted to a highly specific abiotic habitat regime with regard to elevation, aspect, slope, or known soil characteristics. Elevation ranges from 1158 m to 2250 m at the locations visited, and aspect is generally southern, although one location has a northwest exposure. Slope typically ranges from 20% to 40%, but some populations occur on nearly level ground. At most locations, P. lemhiensis grows in relatively sandy soils, but the soil below the Visitor's Center at the Battlefield has a great deal of clay in it. In summary, although

general habitat preferences are apparent, P. lemhiensis is probably not restricted to a particular microhabitat which is itself rare.

Sagebrush hillsides that appear to be likely habitat for Penstemon lemhiensis are extensive in southwestern Montana and adjacent Idaho. However, the species occupies only a portion of these seemingly homogeneous hillsides, while species such as Eriogonum umbellatum and Achillea millefolium are ubiquitous. Also, there is similar sagebrush habitat extending well beyond the range of P. lemhiensis into Idaho, Washington, Oregon, and Wyoming. To explain these aspects of the distribution of the species, very specific habitat characteristics must be identified or alternatives to habitat specificity must be sought.

Perhaps the most fruitful approach when attempting to identify specific habitat requirements of Penstemon lemhiensis would be to compare adjacent areas with and without the species. Detailed analyses of the soil and measurements of soil moisture and temperature should be made. Additionally, these parameters should be investigated at all P. lemhiensis locations to determine if they represent a narrow or broad range of requirements. Careful scrutiny of the habitat is needed to discover any other abiotic variables that may affect the occurrence of P. lemhiensis.

To test the hypothesis that the absence of Penstemon lemhiensis in a particular area is regulated by some abiotic aspect of the habitat, transplant experiments could be performed. Monitoring the vigor of plants transplanted to areas with and without P. lemhiensis would provide a measure of their success in the two potentially different types of areas. Germination rates in the two areas should also be investigated by monitoring germination of known quantities of seeds spread over the two areas. If success were equal in the two areas, then alternative hypotheses should be developed; the lack of plants could not be attributed to differences in the proposed microhabitats. These are only very general ideas for experimentation; details of the experimental design need to be refined. Measures of vigor and success require precise definitions, and the elimination of other variables (e.g. differences in vegetation density) is critical.

Reproduction

When suitable habitat is available, it seems unlikely that the population size of Penstemon lemhiensis is limited severely by inefficiencies in reproduction. Evidence for this includes the abundance of plants found in disturbed areas with little vegetation such as ditch banks and roadcuts. Penstemon lemhiensis often dominates at these sites.

However, under certain circumstances and at particular times, maximal reproduction may not be attained. Germination and establishment may be poor in heavily vegetated areas resulting in an absence of plants. Also, pollination levels were lower on the bench where there is a lush growth of grasses than elsewhere at the Battlefield.

Seed dispersal in Penstemon lemhiensis may be restricted to the area immediately surrounding already established plants. Without any obvious mechanisms for wind or animal transport, the seeds are unlikely to be dispersed any great distance. To some extent, poor dispersal could prevent P. lemhiensis from colonizing some isolated areas within its range and beyond its present range. The above speculation is based on casual observations only; the nature of dispersal in P. lemhiensis needs to be documented and compared with dispersal in closely related, more widespread species before its significance can be addressed adequately. The shape of P. lemhiensis and P. cyaneus seeds is quite similar; P. cyaneus seeds may be slightly larger.

The level of pollination in Penstemon lemhiensis may be somewhat limited by pollinator abundance or activity as indicated by the breeding system data collected in 1982. Also, at the Battlefield in 1983, none of the stalks observed were producing seeds on 26 July. The rosettes of

P. lemhiensis plants appeared to be healthy, and flowers, stigmas, and stamens appeared to be normal. By the same time the year before, seed set was clearly detectable at the Battlefield. Normal seed development was noted during three prior days at Lemhi Pass, Argenta, and Badger Pass. It is possible that seed set did not occur at the Battlefield due to developmental problems with reproductive parts or lack of fertilization, but there was no evidence to support this contention. A more reasonable explanation may be that pollination did not occur. Information supplied by residents of the Big Hole suggests that the weather patterns were somewhat unusual during 1983. The winter was relatively mild with little snow, early summer low temperatures dipped into the twenties several times, and then there was a great deal of rain throughout much of the summer. Such weather could have adversely affected some of the pollinators of P. lemhiensis. No insects were seen visiting the flowers at the Battlefield in 1983; vespid wasps were abundant on the inflorescences remaining in bloom at the three other locations visited.

The vespid wasp Pseudomasaris vespoides may be a particularly important pollinator for Penstemon lemhiensis. This possibility needs to be investigated more thoroughly, as well as the relative importance of the other insects observed. The genus Pseudomasaris is restricted in its

distribution to western North America, and the exact distribution of P. masaris could affect the distribution of P. lemhiensis, if the wasp is an important pollinator.

Assessing reproduction as a factor in the distribution and abundance of any rare plant species is a difficult task. First, all aspects of reproduction must be documented. Secondly, if there seem to be inefficient portions of the reproductive cycle, they must be compared with the same reproductive phases in similar, more widespread species. For Penstemon lemhiensis, it is entirely possible that seemingly inefficient reproductive traits are characteristic of members of the genus Penstemon, rather than of rare species per se.

Competition

It appears that Penstemon lemhiensis occurs predominantly in areas with low vegetation cover and is excluded from heavily vegetated areas. Some of the patchy occurrence of P. lemhiensis within its range may be related to this tendency. However, as was emphasized earlier, this is merely a correlation and does not necessarily demonstrate that P. lemhiensis is outcompeted in heavily vegetated areas. Experimentation is necessary to demonstrate that competition is in fact operating. The success of individuals transplanted in areas of gradually increasing

vegetation cover could be monitored. Another approach would be to remove vegetation in a heavily vegetated area (adjacent to an area with P. lemhiensis) and note any seedling establishment. Disturbed areas such as roadcuts and ditchbanks provide interesting settings for natural experiments. Over a period of years, the success of P. lemhiensis could be observed as other species invade the sparsely vegetated sites. If competition is indicated by such experiments, attempts should then be made to identify resources for which competition is occurring and which species are involved in the competitive interactions.

All competition experiments would require controls for potential physical differences in the study sites. Further, if competition is demonstrated, it would be necessary to show that it is a characteristic of Penstemon lemhiensis as a rare species rather than as a member of the genus Penstemon. A preliminary comparison with P. cyaneus suggests that they both occupy areas of low vegetation cover preferentially. Stebbins (1980) argued that there are several genera in western North America, including Penstemon, that are comprised of both rare and common species, all of which are essentially ruderal species.

This type of competition would thus be more likely to explain patterns of abundance within a species' range than outside of its geographic distribution. It is possible, however, that competition could also be a factor in preventing P. lemhiensis from extending its range. If P. lemhiensis is a poor competitor in general, congeneric species (P. cyaneus and P. speciosus) or other ecologically similar species may occupy suitable habitat at the margins of the range and effectively prevent the expansion of the range of P. lemhiensis. Observations at the margins of the ranges would be essential before any hypotheses regarding the importance of competition could be formulated.

Herbivory

Penstemon lemhiensis appears to be susceptible to predation, particularly in the form of consumption of inflorescence stalks by deer and cattle. Herbivory may reduce the potential size of populations in some areas, but it is unlikely that herbivory is significant in restricting the range of P. lemhiensis. Deer are probably fairly evenly distributed in sagebrush habitats throughout the west.

Further comparisons of the degree of herbivory on Penstemon lemhiensis with closely related species are essential. Only one P. cyaneus location was visited, and no browsed stalks were found in 1982. In 1983, there were a few browsed stalks, while the number of browsed P. lemhiensis stalks seemed to be greater. Experiments based on mechanically excluding herbivores would supply useful data. The population sizes of P. lemhiensis and P. cyaneus could be monitored within deer exclosures. A proportionately greater increase in the number of P. lemhiensis individuals would indicate greater susceptibility to herbivory. Along with further field studies, chemical analyses of the stalks should be conducted to reveal any differences in the occurrence of anti-herbivore compounds (alkaloids, terpenes etc.) in the related species. If P. lemhiensis is subject to greater herbivore pressure and if the species lacks anti-herbivore compounds, then herbivory may be associated with rarity within its range.

Evolutionary History

The factors discussed thus far are primarily potential explanations for the within-range rarity of Penstemon lemhiensis. Additional explanations are necessary when considering why the species does not extend beyond its current range in southwestern Montana and adjacent Idaho. This geographical restriction, probably the most prominent

aspect of its rarity, may be largely attributable to the evolutionary history of the species, compounded by aspects of its ecology. It has been suggested that P. lemhiensis arose as the result of hybridization between P. speciosus and P. cyaneus (Keck 1940). For the genus Penstemon in general, most evidence suggests that hybridization has been an important process in speciation events (Clark 1971). Information on the number as well as the meiotic behavior of the chromosomes of the three species would be helpful in evaluating this possibility. Penstemon speciosus appears to be a diploid species with $n = 8$; chromosome counts for the other species have not been published (Clark 1971).

One mechanism that has been proposed for the maintenance of some Penstemon hybrids is pollination by Vespid wasps; the putative parents are pollinated by other Hymenopterans, but not the wasps (Straw 1955). If P. lemhiensis is a recent hybrid, the species may not have had the opportunity to extend its range significantly; suitable sagebrush habitat would already be occupied by the two parental species. Some Penstemon hybrids are rare or restricted in range, but others have become widespread (Clark 1971). After hybridization, differences in habitat tolerances, reproduction, competition, and herbivory might then be important in determining the fate of the three species where they are in contact with one another. The

proposed younger age of P. lemhiensis implies that the species would have had a shorter period of time to adapt and radiate from its point of origin. However, due to habitat destruction, the range of P. lemhiensis may now be contracting rather than expanding.

Genetic Diversity

Genetic diversity in Penstemon lemhiensis is another factor that remains to be investigated. It has been suggested that rare species are genetically depauperate in comparison to more common species. However, any comparisons of genetic diversity between rare and common species suffer from an intrinsic circular argument. As population size decreases, genetic diversity decreases as well. If a rare species is genetically depauperate (and many are not), it can be argued effectively that it is a result, rather than a cause of, small population size. It would be difficult, if not impossible, to distinguish between these two hypotheses. At the very least, the genetic diversity of equal-sized populations of rare and common species should be compared. It is likely, when such populations exist, that there would be no significant differences in the genetic diversity of the two types of species (Stebbins 1980).

This does not negate the importance of the genetic constitution of species, however. Even if there are no appreciable interspecific differences in the number of alleles coding for a particular protein, there may be differences in the actual genes present in each species. The apparently greater ecological amplitude of Penstemon speciosus as compared to P. lemhiensis may have a genetic basis in a greater total number of adaptive genes rather than in a greater number of alleles of the same gene.

CONSERVATION OF PENSTEMON LEMHIENSIS

My study of Penstemon lemhiensis indicates several factors that may be important in determining the distribution and abundance of the species. The preceding discussion of the biological aspects of rarity in P. lemhiensis suggests numerous avenues of research that should be pursued. An experimental and comparative approach is now necessary to produce conclusive results. Identifying the biological basis of rarity is more than an interesting academic pursuit. In many instances, species that become endangered through human activity are those species that have small populations within restricted ranges in their natural state. Most extinctions result from habitat destruction related to human activity, and there are no documented cases of extinction due to competition or predation from native species (Frankel and Soule 1981), but

it is still important to consider these processes. If the biological factors contributing to rarity of a species are known, attempts can be made to minimize additional human-induced pressures on critical characteristics or portions of the life cycle.

The protection of natural habitat, steep sagebrush hillsides in particular, is perhaps the most critical step in the conservation of Penstemon lemhiensis. The hillsides provide habitat that is generally low in vegetation density and may support fewer herbivores such as deer and cattle. On steep hillsides, there is often considerable natural soil slippage, and sagebrush and grasses are not able to dominate as readily there as they are in more level areas. Predation by deer and cattle may be reduced somewhat on hillsides that are steep enough to discourage the animals from traversing the slopes. The deer and cattle may spend a greater portion of time in less steep areas. Cattle grazing should be minimized at all P. lemhiensis locations. Detrimental effects of using the locations as range land include direct impacts such as herbivory and indirect ones such as the invasion and dominance of grasses on overgrazed lands. It is unrealistic to propose that disturbed sites (e.g. roadcuts) are sufficient to preserve P. lemhiensis. It is usually inevitable that weedy species will invade and outcompete most other species. On the Battlefield roadcut,

knapweed (Centaurea maculosa, Asteraceae) has increased in density during the last three years and may continue to increase in density in disturbed areas.

In addition to conserving habitat in general, special consideration must be given to the nature of the Penstemon lemhiensis populations at each of the known locations. The minimum number of individuals necessary for a species to remain genetically viable is currently a point of contention among geneticists and population biologists. Franklin (1980) suggested that an effective population size of 500 is needed to preserve genetic variation in out-crossing species. This figure undoubtedly varies from species to species, but the loss of alleles due to genetic drift is less likely to occur in large populations than in small ones. With several hundred individuals in three areas, the Battlefield location is more likely to support P. lemhiensis in years to come than are locations such as Bannack Pass and Colson Creek with only tens of individuals. Allendorf (1983) noted the importance of trying to maintain high amounts of genetic variation both between individuals within each deme and between different demes. Large population size and migration are important in attaining high levels of genetic variation. This should maximize both the adaptedness of individual demes to local conditions and the evolutionary potential of the species.

Efforts must be made to conserve Penstemon lemhiensis at all known locations, with emphasis on protecting the high number of individuals and subpopulations at locations such as the Battlefield and Argenta. Further, it would be unwise to assume that protecting isolated P. lemhiensis individuals is sufficient. The theory of island biogeography (MacArthur and Wilson 1967) predicts that species diversity will decline as the size of an island decreases and also as the island's distance from the mainland increases. One undisturbed sagebrush hillside amidst many hectares of overgrazed rangeland can be thought of as an island. If this analogy is appropriate, species, including possibly P. lemhiensis, will be lost from the community as the island gets smaller and further isolated from similar native habitat. Unfortunately, known populations are separated by many kilometers of disturbed land and inappropriate habitat already.

In addition to protecting Penstemon lemhiensis and its native habitat, it is imperative to consider any species upon which the plant depends. Penstemon lemhiensis may depend on the Vespid wasp for efficient pollination. The wasp is closely associated with P. lemhiensis while in bloom and may be an important pollinator, both in terms of seed set and cross-pollination. Before any spraying programs are implemented, the effects of herbicides or

pesticides on P. vespoidea, other pollinators, and P. lemhiensis should be determined. The Forest Service has already sprayed in both Montana and Idaho where P. lemhiensis grows.

As was emphasized in the Introduction, rarity is a relative term. Penstemon lemhiensis is rare in the following ways: 1)it is geographically restricted to southwestern Montana and adjacent Idaho, 2)it does not occupy a high percentage of the sagebrush habitat within that range, and 3)it is less abundant than most associated species where it does occur. It is not rare, however, in the sense of extremely narrow endemics that are represented by a few individuals in single populations. The species, therefore, is not critically endangered when compared with such endemics. I believe that Penstemon lemhiensis should be designated as a threatened species.

Nonetheless, the study and conservation of Penstemon lemhiensis are significant endeavors. Experiments can be completed and statistically meaningful data can be collected without threatening the survival of the species. Often this is not the case for the rarest plants. Patterns of rarity may be slightly different or more difficult to discern in moderately rare species, but their utility as experimental organisms may balance such disadvantages. The conservation of species such as P. lemhiensis may be more successful

than conservation attempts with species reduced to a few individuals in a single locality. In most cases, preventing populations from being decimated is more tenable from a biological standpoint than attempting to reestablish viable populations from a few remaining individuals. Many conservation efforts are directed, and justifiably so, toward the most critically endangered species. However, more time and money could be spent profitably on preventing species from reaching the endangered status.

The conservation of Penstemon lemhiensis represents more than protecting a single species. Species interact within communities continually. When one species is subject to drastic reductions in population size or extinction, other species may follow. One estimate was that for every plant that goes extinct, 10-30 other species may also become extinct (Raven 1976). By protecting individual species and their habitats, other species and entire communities are afforded some protection as well. Additionally, Penstemon lemhiensis appears to be part of a complex of regional endemic species that is found in southwestern Montana (Lesica 1983, pers. comm.). When the state is divided into five general floristic regions, 15 of the state's 26 rare, regional endemics (58%) occur in the southwest portion of the state. This southwestern region is characterized by several distinct, arid intermountain valleys that may be the

northernmost extension of a major North American center of endemism in the Great Basin region described by Stebbins (1974).

The importance of conserving species because they are intricate parts of communities or representatives of centers of endemism are sound ecological arguments. Further, many species are of potential importance from the standpoint of medicine, agriculture, or scientific work. Ehrenfeld (1976), however, pointed out the inadequacy of such arguments for species that are unlikely to produce any economic payoff. For such "non-resources", the conservation of a species must be based on esthetic arguments or arguments that all species have an intrinsic right to exist. Whatever rationales are employed, species conservation efforts should continue to be of global concern. Accelerated rates of extinction by human impacts cannot be equaled by any speciation rates known through evolutionary processes.

Appendix 1

Mean Monthly Air Temperature and Precipitation Readings
Battlefield, Montana (1972-1981)

<u>MONTH</u>	<u>TEMPERATURE (degrees centigrade)</u>	<u>PRECIPITATION (cm)</u>
January	-9.9	4.3
February	-7.2	4.1
March	-4.1	2.5
April	0.9	2.3
May	5.6	5.1
June	10.5	4.8
July	14.3	3.6
August	12.7	3.3
September	8.0	3.0
October	3.1	2.0
November	-4.6	3.3
December	-7.9	4.1
	<hr/>	<hr/>
	Mean: 1.8	Total: 16.6

Table adapted from Pierce (1982)

Appendix 2

Angiosperm Species Associated with Penstemon lemhiensis at
 Argenta (A), Battlefield (B), Badger Pass (BP),
 Colson Creek (CC), Lemhi Pass (LP), Bannack Pass (BanP)

ASTERACEAE

- Achillea millefolium L. (B,CC,LP,BP)
Antennaria sp. (B,CC,BanP,A)
Artemisia tridentata Nutt. (All sites)
Aster spp. (B,CC,LP,A)
Balsamorhiza sagittata (Pursh) Nutt.
 (B,CC)
Cirsium sp. (BanP)
Chrysothamnus viscidiflorus (Hook.)
 Nutt. (LP,BanP,A)
Erigeron compositus Pursh (BanP)
Eriophyllum lanatum (Pursh) Forbes (B)
Solidago spp. (B,A)
Taraxacum officinale Weber (BanP)
Tragopogon dubius Scop. (B,LP)
Hieracium cynoglossoides Arr.-Tour. (B)

BORAGINACEAE

- Lithospermum ruderale Dougl. (B,A)

CAPRIFOLIACEAE

- Symphoricarpus albus (L.) Blake (CC)

CARYOPHYLLACEAE

- Arenaria sp. (B,A,BP)

CRASSULACEAE

- Sedum spp. (B,CC)

ERICACEAE

- Arctostaphylos uva-ursi (L.) Spreng. (B)

GENTIANACEAE

- Frasera albicaulis Dougl. (B)

GERANIACEAE

- Geranium viscosissimum F. & M. (B,LP,A)

HYDRANGEACEAE

- Philadelphus sp. (CC)

HYDROPHYLLACEAE

- Phacelia sp. (CC)

LEGUMINOSAE

- Lupinus sp. (All sites)

ONAGRACEAE

- Epilobium sp. (CC)

POACEAE

- Agropyron spicatum (Pursh) Scribn. &
 Smith (B)
Bromus commutatus Schrad. (A)
Bromus inermis Leys. (LP,A)
Festuca idahoensis Elmer (All sites)
Koeleria cristata Pers. (B,CC)
Poa pratensis L. (LP)
Poa samburgii Vasey (BanP)
Stipa sp. (B)

POLEMONIACEAE

- Collomia linearis Nutt. (CC,BanP)
Gilia aggregata (Pursh) Spreng. (B)

POLYGONACEAE

- Eriogonum umbellatum Torr. (All sites)
Polygonum douglassii Greene (CC)

PRIMULACEAE

- Dodecatheon sp. (CC)

ROASCEAE

- Geum triflorum Pursh (BanP)
Potentilla gracilis Dougl. (B,BanP,LP)
Potentilla glandulosa Lindl. (B,BanP)
Prunus sp. (CC)
Rosa woodsii Lindl. (B,CC,LP,A)
Spiraea sp. (CC)

SCROPHULARIACEAE

- Castilleja sp. (B,CC,BanP,LP,A)
Orthocarpus tenuifolius (Pursh) Benth.
 (B,A)
Collinsia parviflora Lindl. (B,CC,BanP)
Penstemon procerus Dougl. (B, BanP)

LITERATURE CITED

- Allendorf, F.W. 1983. Isolation, gene flow, and genetic differentiation among populations. Pages 52-65 in C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, editors. Genetics and conservation. Benjamin/Cummings, London, England.
- Allendorf, F.W., N. Mitchell, N. Ryman, and G. Stahle. 1977. Isozyme loci in brown trout (Salmo trutta L.): detection and interpretation from population data. Hereditas 86: 179--189.
- Andrewartha, H.G. and L.C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- Ayensu, E.S. 1981. Assessment of threatened plant species in the United States. Pages 19--58 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons Ltd., Chichester, England.
- Ball, D.F. 1976. Site and soils. Pages 279--368 in S.B. Chapman, editor. Methods in plant ecology. Halsted Press, New York, New York, USA.
- Boucher, C. 1981. Autecological and population studies of Orothamnus zeyheri in the Cape of South Africa. Pages 343--353 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Clark, D.V. 1971. Speciation in Penstemon (Scrophulariaceae). Ph.D. thesis, Univ. of Montana. 195 pp.

- Cordell, G.V., Jr. 1971. Climate of Montana. In Climates of the states. Climatography of the United States. United States Department of Commerce Publication No. 60-24.
- Drury, W.H. 1980. Rare species of plants. *Rhodora* 82: 3--86.
- Ehrenfeld, D.W. 1976. The conservation of non-resources. *American Scientist* 64: 648--656.
- Fiedler, P.L. 1983. Biological aspects of rarity in the genus Calochortus Pursh (Liliaceae). *Bulletin of the Ecological Society of America* 64: 117.
- Foster, J. 1964. Studies on the population dynamics of the daisy, Bellis perennis, Ph.D. Thesis, Univ. of Wales.
- Frankel, O.H. and M.E. Soule. 1981. Conservation and evolution. Cambridge University Press, Cambridge, England.
- Franklin, I.R. 1980. Evolutionary change in small populations. Pages 135--149 in M. Soule and B. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts, USA.
- Good, R.B. and P.S. Lavarack. 1981. The status of Australian plants at risk. Pages 81--92 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Gottlieb, L.D. 1973. Genetic differentiation, sympatric speciation and the origin of a diploid species of Stephanomeria. *American Journal of Botany* 60: 545--553.
- _____. 1974. Genetic confirmation of the origin of Clarkia lingulata. *Evolution* 28: 244--250.
- Greig-Smith, J. and G.R. Sagar. 1981. Biological causes of local rarity in Carlina vulgaris. Pages 389--400 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Griggs, R.F. 1940. The ecology of rare plants. *Bulletin of the Torrey Botanical Club* 67: 575--593.

- Harper, J.L. 1981. The meanings of rarity. Pages 189--204 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Harvey, H.J. and T.C. Meredith. 1981. Ecological studies of Peucedanum palustre and their implications for conservation management at Wicken Fen, Cambridgeshire. Pages 365--378 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Henderson, D.M. 1981. Vascular plant species of concern in Idaho. Rare and Endangered Plants Technical Committee of the Idaho Natural Areas Council. University of Idaho Forest, Wildlife and Range Experiment Station Bulletin No. 34, Contribuiton No. 210. Moscow, Idaho, USA.
- Hitchcock, C.L., A.C. Cronquist, M. Ownbey and J.W. Thompson. 1969. Vascular plants of the Pacific Northwest. Part 4, page 365. University of Washington Press, Seattle, Washington, USA.
- Holloway, J.K. 1964. Projects in biological control of weeds. Pages 650--670 in P. Debach, editor. Biological control of insect pests and weeds. Chapman and Hall, London, England.
- Keck, D. 1940. Studies in Penstemon. VII. The subsections Gairdneriani, Deusti and Areiarii of the Graciles and miscellaneous new species. American Midland Naturalist 23: 594--616.
- Keck, D. and A. Cronquist. 1957. Studies in Penstemon. IX. Notes on northwestern American species. Brittonia 8: 247--250.
- Kruckeberg, A.R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. American Journal of Botany 38: 408--419.
- _____. 1957. Variation in fertility of hybrids between isolated populations of the serpentine species Streptanthus glandulosus Hook. Evolution 11: 185--211.
- Langenheim, J.H., B.L. Hackner and A. Bartlett. 1967. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. Botanical Museum Leaflets, Harvard University 21: 289--324.

- Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, Berlin, West Germany.
- MacArthur, R.H. 1972. Geographical ecology: patterns in the distribution of species. Harper & Row, New York, New York, USA.
- MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts, USA.
- Moll, E.J. and A.A. Grubb. 1981. Aspects of the ecology of Staavia dodii in the south western Cape of South Africa. Pages 331--342 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods in plant ecology. John Wiley & Sons, New York, New York, USA.
- Myaitt, R.G. 1968. The ecology of Eriogonum apricum Howell. M.S. Thesis. University of California, Davis.
- Nelson, T.C. 1955. Chestnut replacements in southern highlands. Ecology 36: 352--353.
- Parsons, R.F. and J.H. Browne. 1982. Causes of plant species rarity in semi-arid southern Australia. Biological Conservation 24: 183--192.
- Pierce, J.R. 1982. A floristic survey of the Big Hole National Battlefield. M.A. Thesis, University of Montana, Missoula.
- Prince, S.D. and A.D.R. Hare. 1981. Lactuca saligna and Pulicaria vulgaris in Britain. Pages 379--388 in E. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- Rabinowitz, D. 1981. Seven forms of rarity. Pages 205--218 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.

- Raven, P.H. 1976. Ethics and attitudes. Pages 155-181 in J. Simmons, R. Beyer, P. Brandham, G. Lucas, and V. Parry, editors. Conservation of threatened plants. Plenum Publishing, New York, New York, USA. P; Raven, P.H. and D.I. Axelrod. 1977. Origin and relationships of the California flora. University of California Publications in Botany: 721--134.
- Sagar, G.R. and A.M. Mortimer. 1977. An approach to the study of the population dynamics of plants with special reference to weeds. Applied Biology 1: 1--47.
- Salisbury, E.J. 1926. The geographical distribution of plants in relation to climatic factors. Geographical Journal 67: 312--335.
- Salisbury, F.B. and C.W. Ross. 1978. Plant physiology. Wadsworth Publishing Co., Belmont, California, USA.
- Skinner, B.R. 1979. Locations and site requirements of three endangered threatened Missouri glade plant species. M.S. Thesis, University of Missouri, Columbia.
- Skinner, B.R., G.E. Probasco and F.B. Samson. 1983. Environmental requirements of three threatened plants on limestone glades in southern Missouri. Biological Conservation 25: 63--74.
- Stebbins, G.L. 1942. The genetic approach to problems of rare and endemic species. Madroño 6: 240--258.
- _____. 1974. Flowering plants: evolution above the species level. Harvard University Press, Cambridge, Massachusetts, USA.
- _____. 1980. Rarity of plant species: a synthetic viewpoint. Rhodora 82: 77--86.
- Straw, R.M. 1955. Hybridization, homogamy and sympatric speciation. Evolution 9: 441-444.
- Synge, H., editor. 1981. The biological aspects of rare plant conservation. John Wiley & Sons, Ltd., Chichester, England.
- United States Department of the Interior. 1980. Endangered and threatened wildlife and plants: review of plant taxa for listing as endangered or threatened species, December 15, 1980. Federal Register 45(242): 82480--82569.