REPRODUCTIVE ASPECTS OF LOMATIUM BRADSHAWII AND ERIGERON DECUMBENS OF THE WILLAMETTE VALLEY, OREGON

by

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A THESIS

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L. bradshawii and *E. decumbens* are two rare plants endemic to the Willamette Valley, Oregon. They are members of a prairie ecosystem that has been greatly diminished by human activity in the valley. This research measured pollen and seed dispersal in both species to estimate neighborhood area and size. Pollen dispersal was measured indirectly by measuring the flight distance of pollinating insects. A variety of insects were observed pollinating each species. Seed dispersal was measured directly for *L. bradshawii* and estimated for *E. decumbens*. Models of pollen carryover were used to modify the calculated neighborhood areas. Under three models of pollen carryover, *L. bradshawii* neighborhood areas ranged from 40 m^2 to 227 m^2, and neighborhood sizes ranged from 17 to 95 individuals. Using the same models, *E. decumbens* neighborhood areas ranged from 36 m^2 to 86 m^2, and neighborhood sizes ranged from 11 to 26 individuals.

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DEDICATION

This work is dedicated to Ruth Martin Jackson, a long-time appreciator of flowers.

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CHAPTER I

INTRODUCTION

The Willamette Valley of Oregon once supported an extensive prairie ecosystem (Habeck, 1961). At least two distinctive communities are known, an upland prairie and a wet prairie. These prairies differ from the prairies of the Midwestern United States, in terms of vegetation and climate. Both wet prairie and upland prairie ecosystems were somewhat dependent on fire disturbance. Without the presence of fire, prairie areas would give way to woody plants in the Willamette Valley (Frenkel and Heinitz, 1987).

The history of fire in the Willamette Valley has three stages: prior to human habitation; Kalapuya habitation; and settlement by Euro-American pioneers. The frequency of fire in the valley prior to human habitation is unknown, but it likely that fires were not uncommon on the prairies. The ancestors of the Kalapuya Native Americans inhabited the valley more than 8,000 years ago (Scovell, 1978). They used fire as a tool, intentionally burning large parts of the Willamette Valley for a variety of reasons, mostly related to the procurement of food (Boyd, 1986). In the late 1800's, Euro-American settlers arrived in the Willamette Valley. They suppressed fires, and began converting prairies to agricultural uses. Since that time, the prairies of the valley have declined greatly in area.

Today, prairies in the Willamette Valley are greatly decreased in area and in general health, and efforts are underway to restore these ecosystems. Patches of remnant prairie are rare, fragmented, and inhabited by invasive exotic plants (Christy and Alverson, 1994; Wilson, 1995). These communities support rare plant species, several of which are endemic to the Willamette Valley. Under these conditions, a variety of private and governmental agencies are attempting to manage and restore native prairies. Many of the techniques and tools for management are employed without the benefit of scientific research. The prairie communities of the area are quite distinct from other prairie systems in North America, limiting the applicability of research from those regions. It is hoped that this research into the reproductive biology of two prairie plants might benefit resource managers.

Two Willamette Valley prairie plants were selected for study of effective population sizes and neighborhood areas. *Lomatium bradshawii*, Bradshaw's lomatium, is the only federally-listed endangered plant in the Willamette Valley (Parenti, *et al.*, 1993). The plant is endemic to the valley, where it grows in wet prairies. *Erigeron decumbens* var *decumbens*, the Willamette daisy, is also endemic to the Willamette Valley. (Below, this plant will be referred to as *Erigeron decumbens*, or *E. decumbens*.) It is a Category 1 Candidate for listing on the federal endangered species list. These two plants were selected as study species because of their rarity, the distinctiveness of their habitats, and their proximity to one another. Because of their fragmented habitat and small populations, these plants may experience reproductive difficulty. It is the reproduction of these plants that will be the focus of this research.

Gene flow between individuals of a sexually-reproducing species is a requisite for the species continued survival. Sewall Wright (1946, 1969) developed a concept of an neighborhood size, a measure of the number of individuals in a population that can actually be expected to breed randomly. This is often much smaller than the actual size of the population. For example, deer may exist in one continuous population throughout a rural area many kilometers wide. If there is no discrete barrier to deer movement through the area, the deer can be considered part of one population. However, one would not expect an individual to mate with another individual 250 kilometers away. The actual number of individuals within that population that could be expected to breed randomly is the effective size of the population. The area in which all the individuals in the effective size of the population live is called the neighborhood area. For plants, the neighborhood area is based on the two methods that plants have of moving genetic material: pollen dispersal and seed dispersal. Estimates of neighborhood size and area can provide critical information for resource managers. Neighborhood size estimates can indicate the potential risk of inbreeding that a small population faces. Neighborhood area estimates can show which individuals may be considered a part of a population, and what spatial arrangements would be necessary to form large, genetically-linked populations.

The objective of this research was to develop estimates of neighborhood area for *L. bradshawii* and *E. decumbens*. These calculations, combined with density measurements, provide estimates of neighborhood size. Measurement of neighborhood area will also lead to greater information regarding the pollinating insects of both study species and their behavior.

Neighborhood area can indicate whether discrete patches of plants can exchange genetic material or are separate sub-populations. Neighborhood size, as a measure of the number of potential mates for an individual, can indicate the likelihood of inbreeding. This information can be used to make management decisions.

In order to estimate the neighborhood areas of these plants, their pollen and seed dispersal mechanisms were studied. Both plants have pollen that is moved by insects. It was assumed that insect pollination accounted for the majority of pollen movement. Pollen movement was calculated from field observations of insect flight distances between flowers. Models were employed to express pollen carryover, the possibility that pollen gathered from one flower might travel beyond the next flower visited. For *L. bradshawii*, seed dispersal was also measured in the field. For *E. decumbens,* this was not possible, and seed dispersal was predicted based on a measurement of the falling speed of the seeds, the height from which seeds were released, and wind data during the time of year when the seeds fall.

The data on pollen dispersal and seed dispersal were combined to calculate neighborhood areas for these two rare species. Neighborhood areas and plant densities were used to calculate neighborhood size.

For *L. bradshawii,* neighborhood areas were found to range from 39.64 m^2 to 227.17 m^2 under different pollen carryover models. Density of the plant was found to be .42 plants per m^2, so the population size was found to be 17 to 95 individuals. For *E. decumbens*, neighborhood areas were found to range from 36.12 m^2 to 85.80 m^2. A density measure from other researchers was used, with a value of 0.3 plants per m^2, so the population size was found to be 11 to 26 individuals. Compared with other research, these neighborhood areas are of moderate size, but the neighborhood sizes are small enough to indicate potential inbreeding problems.

Although population dynamics vary among years and sites, these calculations may help provide a baseline of information for resource managers and future researchers of the reproductive biology of both species.

CHAPTER II

DESCRIPTION OF RESEARCH PROBLEM

This research involves *Lomatium bradshawii* and *Erigeron decumbens*, two plants endemic to prairies of the Willamette Valley of Oregon. Prairies were once the dominant ecosystem of the valley, but in the last 150 years, human activity in the valley has greatly reduced and fragmented the areas of prairie. The natural history of the Willamette Valley may help explain how the prairie ecosystems developed. More recent history of human activity in the valley explains how the species' populations have declined. Today, the prairie remnants are generally small, isolated from other remnants, and threatened by exotic species. As a result, many of the plants that inhabited these prairies are now rare and face some threat of extinction. In these circumstances, efforts have begun to preserve and restore prairie habitat. This research may help these efforts.

Description of Study Area

Geomorphology of the Willamette Valley

The Willamette Valley is the drainage of the Willamette River, which drains into the Columbia River near Portland, Oregon. (See Figure 1.) The Willamette flows north, draining a 31,200 square kilometer area between the Cascades and the Coast Mountain Range. The valley stretches 200 kilometers north-to-south, from Portland to Cottage

Grove, and ranges 30 to 50 kilometers wide. In the valley, alluvial flats are separated by sets of low hills. Elevation is 50 meters at Salem, and 129 meters at Eugene, 130 kilometers south. The Willamette River is anastomosed or meandering through most of the valley, although the channel is straighter in the northern portion of the valley than the south (Franklin and Dyrness, 1973). The valley floor contains thick alluvial deposits, which are the result of flooding in the Pleistocene.

Theories about the flooding of the Willamette Valley vary, but it is generally accepted that the valley did flood during the Wisconsinan Period. McDowell (1991) provides a good summary of research on flood history. Flooding probably occurred in two phases. The first phase was characterized by multiple flood events. These floods occurred as a result of damming or hydraulic ponding of water in the area of Portland, Oregon, that caused flow to spill into the Willamette Valley. Each spill-over event may have caused a temporary lake that deposited silty to sandy deposits over the floor of the Willamette Valley. The second phase of flooding was a single, catastrophic flood event that brought more water into the Willamette Valley than individual events in the previous phase of flooding, with lake waters reaching elevations of 122 meters. The second phase of flooding caused silty, low-energy deposits. One hypothesis suggests that the first phase of flooding began in the middle Wisconsinan Period, and the second phase occurred in the late Wisconsinan. A second hypothesis suggests that both phases occurred during the late Wisconsinan Period. The lake formed by this second phase drained around 13,000 years ago (McDowell, 1991). The lakes that formed in the Willamette Valley caused the present-day valley floor to be quite flat, as a result of lake

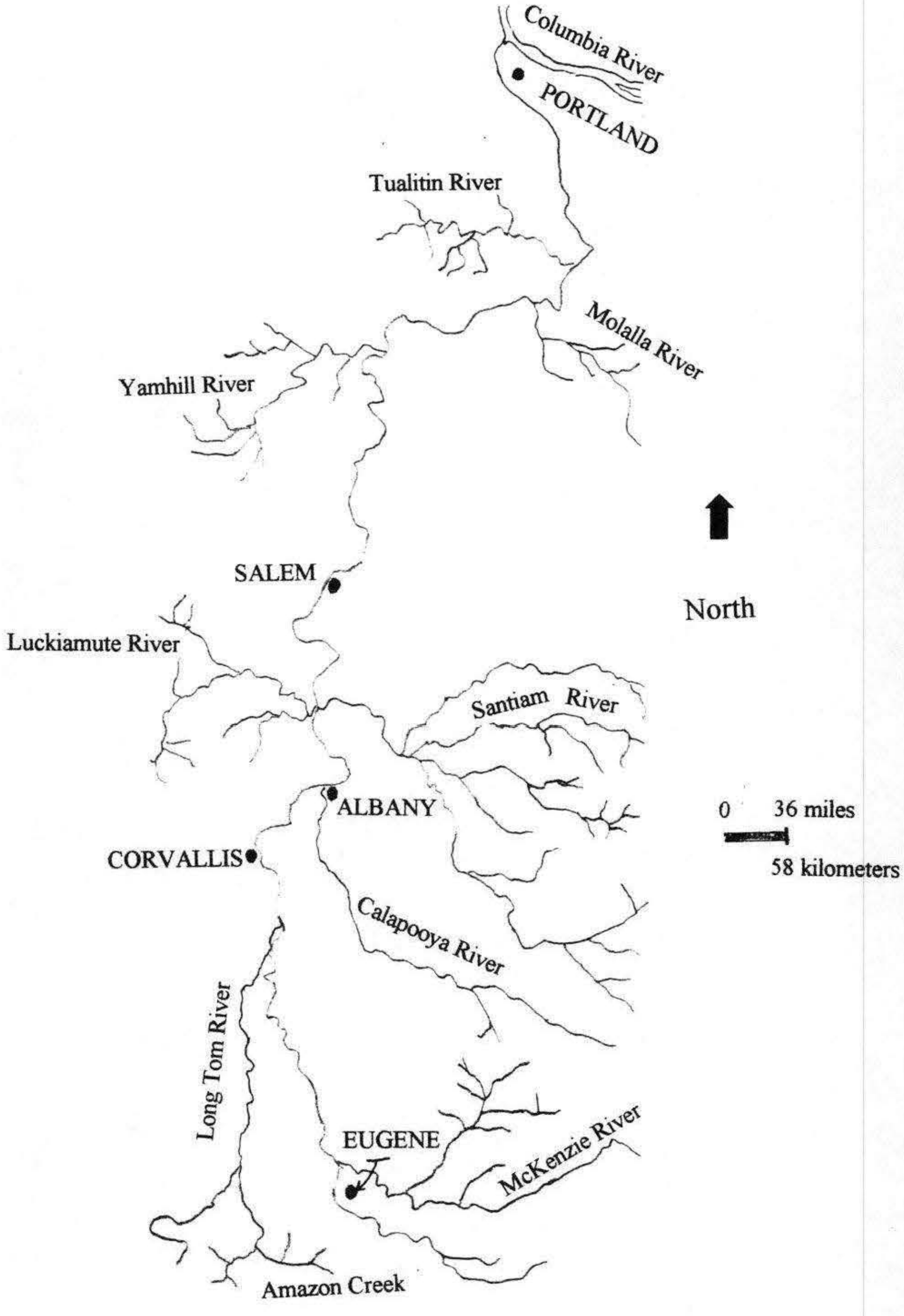

Figure 1. The Willamette Valley, Oregon (adapted from Johannessen, et al., 1971).

deposits. Also, many of these present-day flat surfaces are clayey, partially due to the mode of deposition and partially due to post-depositional soil formation (P. McDowell, 1996, personal communication). These conditions of flat surfaces and relatively impermeable clayey soils, combined with high annual rainfalls, result in extensive areas that are suitable for prairie species that depend on wet soil conditions.

Prairies of the Willamette Valley

The Willamette Valley once supported extenisve areas of prairie and oak savannah (Habeck, 1961). Fire has been a component of the Willamette Valley ecosystems since the last ice age, and has been important in preventing woody species from establishing in prairies. Prairie remnants that exist today are fragmented due to land-use modifications and degraded by introduced species. This makes it difficult to understand the plant species and their frequencies as they existed when the prairies were large and healthy. Therefore, early botanical works in the Willamette Valley provide crucial information about what species may have composed prairies in the past.

Plant communities in prairie ecosystems vary mainly due to differences in moisture. Moisture differences, in turn, are due to elevation, slope, and permeability of soils. Several researchers have developed different schemes for classifying the prairie ecosystems of the Willamette Valley. Their schemes will be discussed below. For the purposes of this research, Willamette Valley prairies will be divided into two basic categories, wet prairie and upland prairie. Wet prairies occur in areas of low relief, with poor drainage and hydric, clayey soils. Wet prairies are dominated by a bunch-grass, *Deschampsia cespitosa.* The widely-used term upland prairie is misleading, because the soil types of these areas are not consistently upland soils, and because these ecosystems can occur on the valley floor. Some of the upland prairies occur on colluvium, which is upland soil, but some occur on terraces, alluvium, and even floodplain soils, which are not upland soils (Wilson, *et al.*, 1993; Clark, *et al.*, 1993; Soil Conservation Service, 1987). The upland prairies are really characterized only by drier conditions due to better draining soils or topography, and by vegetation that thrives in these conditions. A better term for these areas would be mesic prairies. However, the term upland prairie has become established in the literature, and that convention will be followed here, in order to avoid confusion. Upland prairies contain a variety of grasses and forbs.

The division of Willamette Valley prairie into wet prairie and upland prairie is useful because of different plant communities and different land uses. Up to 1600 km^2 (400,000 acres) of the Willamette Valley prairie was wet prairie, and 2400 km^2 (600,000 acres) was upland prairie (Franklin and Dyrness, 1973; Johannessen, *et al.*, 1971). Currently, prairies occupy less than one percent of their original extent in the Willamette Valley. As evidence of their scarcity, Habeck (1961) was unable to locate any prairie relics at all. Wet prairie currently exists on less than 5 km^2(1000 acres) of the valley, 0.25% of its original extent (Christy and Alverson, 1994). No data are available on the current extent of upland prairie, but land use patterns and personal observations suggest that upland prairie may be rarer today than wet prairie. The communities of upland and wet prairies observed in this research are some of the least disturbed remnants, and most closely resemble the earliest description, that of Nelson (1919).

Prairie communities developed in the Willamette Valley sometime after the last ice age. This ice age reached its glacial climax around 15,000 to 14,000 years ago, and eventually ended around 10,000 years ago (Whitlock, 1992). Prairie vegetation was able to establish once glacier-influenced flooding ended around 13,000 years ago. Studies of fossil pollen grains from lakes near the Willamette Valley show that pollen from prairie-type plants increased, indicating prairie ecosystems were well-established by 9500 years ago (Barnosky, 1985). From the end of the ice age, fire has been a part of the ecosystem, until the past 150 years, when Europeans began to suppress fire. In the absence of fire as a disturbance, the wet prairie generally gives way to a climax *Fraxinus latifolia* (Oregon ash) forest community (Frenkel and Heinitz, 1987), although in some of the wetter areas, woody vegetation cannot establish even in the absence of fire (Lippert and Jameson, 1964). Disturbance, in the form of wildfires, favored the wet prairie community over a *Fraxinus latifolia* forest community. The Willamette Valley experiences a long, dry summer, and wet prairies are very dry, and fire-susceptible, in late summer and early fall.

Fire, from natural and human sources, has been crucial to the formation and maintenance of the Willamette Valley prairie. Little is known about the frequency of fire in the valley prior to human habitation. The Native Americans of the Willamette Valley are the Kalapuya, whose ancestors were present in the valley as long as 8,000 years ago (Scovell, 1978). The Kalapuya used fire as a land management tool, which incidentally supported the prairie community at the expense of a *Fraxinus latifolia* forest community. Prior to settlement by Europeans, native Kalapuya people intentionally burned the prairies. Their main reasons for burning included the use of fire to surround herds of deer in communal hunts and to gather tarweed (*Madia* species) seeds after burning away both surrounding grasses and the tar-like pitch on the plants. Other reasons included the gathering of grasshoppers and opening of ground beneath oak trees to facilitate acorn harvesting (Boyd, 1986). Their activities created frequent disturbances that maintained prairie communities. Journals of pioneer explorers and settlers detail extensive burned areas as a result of Kalapuya fire use (Johannessen, *et al.*, 1971).

The arrival of European settlers in the Willamette Valley began a period of rapid changes in land use practices. These changes gradually reduced the acreage of prairie in the valley. In the 1800's, the pattern of prairie burning was disrupted by European settlers, who converted drier portions of the valley to agriculture. Upland prairie lands were among the first lands farmed (Towle, 1982). In some areas initially too wet for agriculture, settlers dug ditches to drain the prairies. Some places remained unaltered because they were too wet even with alteration. In much of this area, the absence of fire caused the invasion of woody plants, and the prairie converted to woodlands. A soil survey of Linn County, Oregon conducted in 1929 reported that "probably more than 90% (of level prairie land) has at one time or another been in cultivation, but owing to poor drainage conditions many of the fields have been abandoned. At the present time about 35% of the land is in cultivation and the remainder is in weeds and grasses with small patches of wild rosebushes and scrub oak." (Kocher, 1929, pp. 49-50). In the 1950's and 1960's, flood control projects, such as dams and channel "improvements" that involved straightening and simplifying rivers and streams, allowed still more of the wet prairie to be converted to agriculture (Christy and Alverson, 1994). In 1939, grass seed production began in the valley. Unlike other crops, many grass seeds actually preferred the heavy, soggy clay soils of the prairies. This enabled profitable farming of areas where soils may have been too poor to farm vegetable crops. Annual burning of the stubble of grass-seed fields began in 1948 in order to control diseases. By the 1970's, over 1200 km^2 (300,000 acres) were on some schedule of controlled burning (Towle, 1982). This burning has decreased in recent years, due to state legislation resulting from public protests over health and safety threats, pollution, and aesthetics (Hege, 1995; Associated Press, 1993).

Early records may mention vegetation of the valley in vague and non-botanical terms, but these records are still invaluable descriptions of the composition and extent of ecosystems that no longer exist in pristine form. The original vegetation of the valley has undergone significant changes, and it is clear that prairies have decreased greatly in their extent. Government land survey records from the 1850's provide the earliest records of vegetation patterns in the valley. These records suggest that most of the valley was prairie and oak savannah at that time (Habeck, 1961). The floor of the valley has an area of over 6500 square kilometers (1.61 million acres) (Patterson, Langford, and Stewart, 1971). Of this area, over 4000 km^2 (nearly 1 million acres) may have been covered with prairie vegetation (Franklin and Dyrness, 1973).

Because both wet prairie and upland prairie have been altered extensively following European arrival in the valley, original community composition is a matter of guesswork. Over the past 140 years, various descriptions have been written of the prairie species. These descriptions vary somewhat in their division of communities and the dominant species described in these communities. Early reports were less scientific and comprehensive, but remain valuable due to the changes that have occurred since their time. Changes in species composition from these early reports to later reports may be a result of changes in community composition, rather than variability in the sites examined or the biases of researchers.

Early reports of the plants of the Willamette Valley vegetation indicate that grasslands were common in the valley in the 1800's and early 1900's. The land surveys of the 1850's were intended to be a general land survey, not a botanical survey. However, surveyors generally described the vegetation they encountered. Also, the surveyors tended to look for trees to make into survey markers, and the amount of difficulty they had finding trees can indicate the frequency of trees in the landscape. These surveys merely describe the flora of the prairies as "grasses", "ferns", and "weeds" (Habeck, 1961).

In 1919, Nelson made the first botanical list of grassland species in the Salem, Oregon vicinity. He detailed 106 species, of which 55 were introduced, and 51 were natives (Nelson, 1919). His hydrophyte society is dominated by *Deschampsia cespitosa*, a bunch-grass. Other grass species that were likely a part of the hydrophyte community include *Agrostis aequalis*, *Beckmannia syzigachne*, *D. danthonioides*, *Eragrostis hypnoides*, *Glyceria leptostachya*, *G. occidentalis*, *G. pauciflora*, *Leersia oryzoides*, *Panicum capillare* var. *occidentalis*, *Pleuropogon refractus*, *Poa triflora*, and *Trisetum cernuum* (Habeck, 1961). In upland prairies, which Nelson called "xerophyte societies," likely grass species include *Agrostis halli*, *Agropyron pauciflorum*, *Bromus carinatus*, *B.*

vulgaris, *Danthonia californica*, *Elymus glaucus*, *Festuca octoflora*, *F. californica*, *F. rubra*, *F. occidentalis*, *F. subulata*, *F. idahoensis*, *Hierochloe occidentalis*, *Panicum scribnerianum*, *P. pacificum*, *Poa scabrella*, *P. howellii*, *Sitanion jubatum*, *Stipa lemmoni*, and *Trisetum canescens* (Habeck, 1961). A more recent researcher has agreed with this list of upland prairie species, and has suggested that the dominant native species were probably grasses such as *Festuca rubra*, *Elymus glaucus*, and *Bromus carinatus* (C. Schultz, 1995c, personal communication).

Turner (1969) examined species composition at several sites within a 15 km radius of Corvallis, Oregon. He identified three grassland communities, and named some different species as dominant than those named by Nelson. All of his sites, however, may be better drained than wet prairies described by Nelson (1919). In Turner's descriptions, the wettest community was dominated by *Festuca rubra*, the intermediate community was dominated by *Danthonia californica*, and the driest community was dominated by *Stipa occidentalis* var. *minor*. Over all his sites, *Elymus caput-medusae* and *D. californica* were the most common species (Turner, 1969).

More recently, Moir and Mika (1972) developed a different division of the prairie communities of the Willamette Valley. They analyzed prairie species composition near Corvallis. They identified three major communities, a tall-grass prairie, a shrub thicket, and a short-grass prairie that occurs at transitions between the other two communities. On the lower and flatter areas, a tall-grass grassland dominated by *Deschampsia cespitosa* grew. This community is similar to the wet prairie described by Nelson (1919). Other major species included *Holcus lanatus*, *Poa ampla*, *Juncus* species, *Danthonia* *californica*, and *Bromus japonicus*. Areas somewhat lower and wetter included *Hordeum brachyantherum*, *Beckmannia syzigachne*, and *Alopecurus geniculatus*, and areas somewhat higher and drier included *Camassia quamash*, *Montia linearis*, and *Eleocharis acicularis*. On hummocks within the prairie, shrub thickets grew dominated by *Rosa eglanteria*. Other important species here included *Crataegus douglasii*, *Amelanchier alnifolia*, *Rhamnus purshiana*, *Rhus diversiloba*, and *Symphoricarpos albus*, and *Sidalcea campestris*. Between these two communities grew a shorter community dominated by *Poa pratensis* and *Agrostis* species. Other important species included *Danthonia californica*, *Festuca partensis*, *Carex* species, *Geranium dissectum*, and *Aster chilensis*. In all of these communities, *Fraxinus latifolia* was observed to be invading, suggesting that fires had been necessary to maintain these communities (Moir and Mika, 1972).

Environment and Ecology of Willamette Valley Wet Prairie

Wet prairie formed in the valley by virtue of flat terrain, clayey soils, and disturbances. Wet prairies are found in lower and flatter areas of the valley, and have always been lesser in extent than upland prairie. These wet prairies are different from the wet prairies of the American Midwest, in that they are found on relatively impermeable soils and are precipitation-fed. Thus, these wet prairie need not be adjacent to flowing water, or even low in elevation. Also, the great seasonal variation in precipitation in the Willamette Valley requires that the plants of the wet prairie tolerate significant summer water deficits. In addition to the permanent wet prairie areas formed by flat ground and relatively impermeable soils, wet prairie was found in areas of natural and man-made disturbances, such as oxbow lakes, meander scars of creeks, ditches, and excavations (Lippert and Jameson, 1964). These disturbances gradually fill in, and continuous sediment deposition decreases the average water levels. Plant community composition within the wet prairie is controlled primarily by the amount of moisture in or on the soils. The change in plant communities from the wettest habitats to the driest habitats in permanent wet prairie mirrors the change in community composition over time in temporary wet prairie. Distinct communities exist from seasonal ponds to grasslands on moist soils.

Heavy winter precipitation and poor soil drainage cause standing water on vegetated surfaces in much of the wet prairie. Lippert and Jameson (1964) described the successional stages from wetter to drier areas of wet prairies, further differentiating the community described by earlier researchers (Nelson, 1919; Moir and Mika, 1972). The driest of the wet prairies, and the climax of succession in disturbed areas, is a grassland-composite stage. This stage is dominated by *Deschampsia cespitosa*, tufted hair grass; *Agrostis alba*, redtop; and *Holcus lanatus*, western wild oat grass (Lippert and Jameson, 1964). Wet prairie communities are quite diverse. The Nature Conservancy's Willow Creek Preserve in Eugene has over 200 plant species and may contain 30 plant species per m^2 (Christy and Alverson, 1994). *D. cespitosa* forms hummocks up to 45 cm (1.5 feet) tall, which provide its roots with oxygenated soil and form micro-habitat for other organisms. In winter, there may be 5 to 10 cm (2 to 4 inches) of water standing between *D. cespitosa* hummocks (Christy and Alverson, 1994). The two plants examined in this study, *Lomatium bradshawii* and *Erigeron decumbens*, are members of this community. *L. bradshawii* grows only in the wet prairie grassland, but *E. decumbens* also grows in upland prairie habitats.

The wet prairie of the Willamette Valley is of particular biological value because of the numerous rare species it contains, and the important function it provides for migratory birds. The wet prairie community includes several plant species of special legal status. The most well-protected is *Lomatium bradshawii* (Bradshaw's lomatium), which is listed as endangered under the federal Endangered Species Act. It is currently the only endangered plant endemic to the valley. *E. decumbens*, the Willamette daisy, is a Category 1 Candidate species, which means that there is sufficient information to warrant a listing. A status report on this plant recommends that it be listed as endangered under the federal Endangered Species Act (Clark, *et al.*, 1993). *Sidalcea nelsonia*, Nelson's checkermallow, is currently listed as threatened. In addition, *Aster curtus*, the white-topped aster; *Montia howellii*, Howell's montia; and *Lupinus sulphureus* var. *kincaidii*, Kincaid's lupine, are listed as Category 2 Candidates, meaning that additional information is needed before listing can occur. *Delphinium pavonaceum*, peacock larkspur, is a Candidate, as is *Horkelia congesta* var. *congesta*, shaggy horkelia. *H. congesta* is a species of concern under the Oregon Endangered Species Act, and *Microcala quadrangularis*, timwort, is listed by the Oregon Natural Heritage Program as a species endangered or threatened in Oregon (although it may be more common elsewhere). Of these rare species, *L. bradshawii*, *E. decumbens*, *S. nelsonia, A. curtus*, *M. howellii*, *D. pavaenocium*, *H. congesta*, and *M. quadrangularis* are found in wet prairies. *E. decumbens*, *A. curtus*, *L. sulphureus*, are found in upland prairies (Wilson, *et al.*, 1993; Parenti, *et al.*, 1993).

Other endemic plants include *Aster hallii*, *Sidalcea campestris*, *S. cusickii*, and *Cardamine penduliflora* (Parenti, *et al.*, 1993). The only special status animal in the study area is *Clemmys marmorata*, the Western pond turtle. *C. marmorata* was recently rejected for the federal Endangered Species List, but is clearly struggling to survive in the Willamette Valley. A program is underway to raise young turtles in captivity, and release them at a safer stage of their life-cycles (Stahlberg, 1995).

Some animals, such as waterfowl, require wetlands complexes that have a mixture of wetter and drier habitats. They use different habitats for different functions, such as overnight nesting, feeding, and courtship or at different times of the year (Galatowitsch and van der Valk, 1994). In the Willamette Valley, the wet prairie is an important feeding area for waterfowl (Galen and Lev, 1991). Because the only areas to survive as wet prairie were the very wettest, this diversity of habitat is absent or severely fragmented in most of the Willamette Valley. The valley is an important part of the western route for migratory waterfowl through the United States, because high-quality habitat becomes more scarce to the south.

A survey of the 42 wetland sites near Eugene, Oregon found 13 species of waterfowl using the area during the winter and spring. Large winter ponds at least 6 inches deep attracted the greatest concentration of birds. Many individuals were observed to fly to larger ponds, Fern Ridge Reservoir, or the Willamette River at night, probably to roost in an area with greater protection from predators (Galen and Lev, 1991).

Environment and Ecology of Willamette Valley Upland Prairie

The upland prairie of the Willamette Valley was more wide-spread than the wet prairie prior to human activity in the valley. However, it was also the most desirable land for agriculture for early European-American settlers. Thus, these areas were the first to be converted to grazing and crop production. Today, fewer remnants of upland prairie exist than of the wet prairie. Also, legal emphasis on the protection of wetlands has led to interest in research and acquisition of wet prairie parcels, but no similar interest has been sparked for upland prairie. For these reasons, little is known of the original ecosystems and their component species.

Undisturbed upland prairie communities most likely included the plants described above by Nelson (1919). The least disturbed upland prairies found today are dominated by introduced species (Wilson, *et al.*, 1993). The upland prairies remnants currently surviving most closely resemble the descriptions of Nelson (1919) and C. Schultz (1995c, personal communication). (See Prairies of the Willamette Valley above.)

One plant of the upland prairie is of particular importance because of its relationship to a rare butterfly. *Lupinus sulphureus kincaidii*, Kincaid's lupine, grows only in the upland prairies of the Willamette Valley. It is the sole larval food source for *Icaricia icariodes fenderi*, Fender's blue butterfly. The destruction of upland prairie has diminished the populations of both species. Once thought extinct, *I. icariodes fenderi* has been rediscovered, but has less than 4000 individuals remaining (Schultz, 1995a).

The plight of this butterfly may aid the restoration of upland prairie. One researcher has been working for two years to develop techniques for restoring upland prairie and butterfly habitat (Schultz, 1995b). (See Prairie Restoration Attempts below.)

Threats to Willamette Valley Prairie

Major threats to the prairie are caused by humans, either directly or indirectly. The major direct threat is conversion and draining of wetlands for agriculture or urban uses. Other threats include fragmentation of habitat, introduced species, and global environmental threats.

The original prairies of the Willamette Valley were ideal for agriculture and grazing. Both upland and wet prairies required much less labor to prepare than forested land, which would have required clearing. Upland prairies required only tilling to begin agriculture, and could be grazed with no preparation. Wet prairies were often drained by ditches to facilitate agriculture or grazing. Conversion of wet prairie to agriculture has largely ended in the valley. Most land that could be used for agriculture has been already converted. Older abandoned drainage ditches are slowly filling in, and native species are returning to fields that are no longer in production. However, the native species do not return quickly or completely, and the resulting community is generally less diverse and resilient than undisturbed communities. Near Eugene, a ryegrass field (presumably) that has been abandoned for over twenty years is now high in diversity and abundance of native species, although exotic species still occur in abundance (J. Beall, 1994, personal communication). In other fields that have been out of production for five or six years, exotic species still comprise over 90% of the vegetative cover (personal observation).

Conversion of prairies due to urbanization is currently a major threat to the prairie. By 2012, the population of the Willamette Valley is expected to have increased by over 600,000 people from 1990 census counts, and the land devoted to urban uses is expected to increase by 59% (Community Planning Workshop and the Institute for a Sustainable Environment, 1994). Major portions of the remnant wet prairie are located in the Eugene-Springfield metropolitan area, which has a population of 200,000 (Lane Council of Governments, 1992). Urbanization affects wetlands when sites are drained or filled for construction, hydrology is altered for flood control, and human activities negatively impact nearby wetlands. Direct conversion of wetlands through urbanization and agriculture are now under tighter control due to federal guidelines limiting the development of wetlands. Federal "no net loss" policy requires mitigation or creation of wetlands for every development on existing wetlands (Want, 1990). Such controls are not available to prevent conversion of upland prairie.

Fragmentation of the wet prairie is of critical concern. The total remaining area of this ecosystem is only around 4 km^2 (1000 acres) (Christy and Alverson, 1994). Most of the wet prairie is in small patches of less than 20 hectares (50 acres) (J. Beall, 1994, personal communication and personal observation). These patches are generally separated by roads, urban areas, or agricultural fields, all of which can pose barriers to species migration. Small separated patches are analogous to islands, because migration from one to the other is difficult, and diversity is less than would be expected if the patches were contiguous. Fragmentation causes a loss of habitat heterogeneity, placing at risk those organisms that require more than one habitat to complete their lifecycles. (Western pond turtles, *Clemmys marmorata*, are one such species, and are rare in the Willamette Valley (Parenti, *et al.*, 1993)). Temperate ecosystems seem more resilient to fragmentation than tropical ecosystems, but this may be because species were eliminated by earlier extensive alterations in temperate regions before they were known to science (Wilcove, *et al.*, 1986). Fragmentation also increases edge effect, as the ratio of area to edge decreases. Edge effects may be particularly significant in wet prairie because organisms can see longer distances than they might in forested ecosystems. Waterfowl that are uncomfortable around human activity will avoid fragmented wet prairie altogether (J. Beall, 1994, personal communication).

Introduced species are particularly problematic in the wet prairie of the Willamette Valley. All known prairie remnants contain exotic plant species, and many are comprised of over 50% exotics (personal observation). Among the most pervasive introduced plant species are *Phalaris canariensis* (reed-canary grass), *Rubus discolor* (Himalayan blackberry), and *Dipsacus sylvestris* (teasel).

Prairie Preservation Attempts

Attempts are being made to preserve the fragmented prairie ecosystems of the Willamette Valley and their rare species. Several government and private agencies are working to obtain prairie parcels, to protect and enhance parcels obtained, and to restore intact prairie ecosystems where land use and introduced species have degraded them. These agencies include the Army Corps of Engineers (ACOE), the Bureau of Land

Management (BLM), various local governments, and the Nature Conservancy. Because of the Clean Water Act, which provides strict protection for wetlands, the preservation of wet prairie is more advanced and widespread than the preservation of upland prairie.

Southern Willamette Valley Prairie Protection Efforts

Significant conservation efforts are already underway to preserve what remains of the wet prairie. Several sites are under the protection of resource management agencies. Probably the most significant holding of wet prairie is around the West Eugene Wetlands Study Area, which contains separated parcels owned by the BLM, the Nature Conservancy, and the City of Eugene. (See Figures 2 and 3.) Other preserves are the Fern Ridge Research Natural Area (ACOE), Willamette Floodplain Research Natural Area (U.S. Fish and Wildlife Service), Long Tom Area of Critical Environmental Concern (BLM), and Jackson-Frazier Natural Area (Benton County). Within the West Eugene Wetlands, the Nature Conservancy owns 142 hectares (350 acres) at the Willow Creek Preserve (Christy and Alverson, 1994).

The West Eugene Wetlands (WEW), located partially within the Eugene city limits, contain important remnants of wet prairie and other habitats. A part of the wetlands has been designated by the BLM and the City of Eugene as the West Eugene Wetlands Study Area (WEWSA). The WEWSA contains 32.38 km^2 (8,000 acres), most of which is privately owned. Some parts of the WEWSA are already developed, and other parts are slated for development. However, over 5.25 km^2 (1300 acres) have been identified as wetlands, mostly wet prairie. The WEWSA is being managed by a

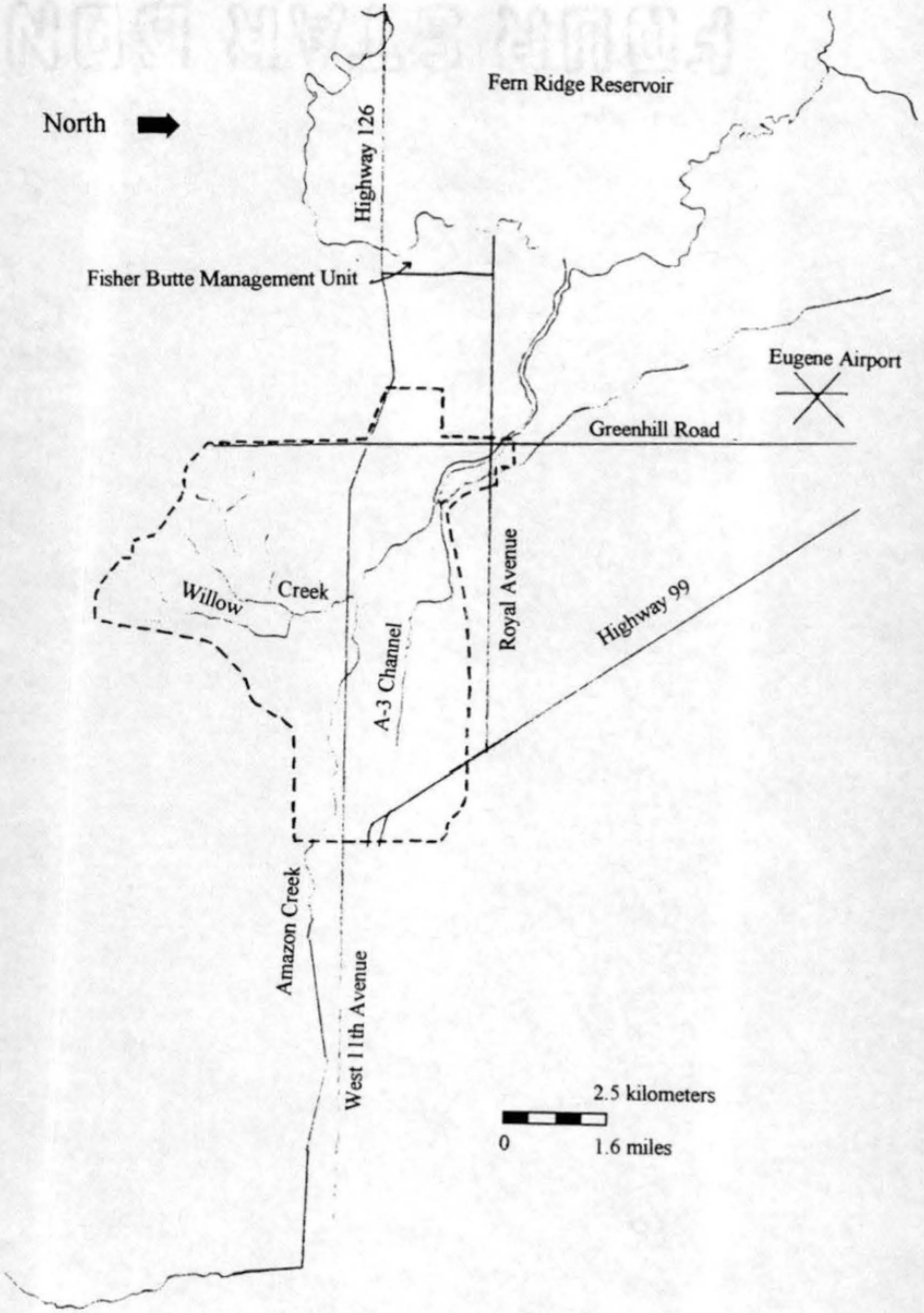

Figure 2. West Eugene, Oregon, and West Eugene Wetlands Study Area (adapted from Lane Council of Governments, 1992).

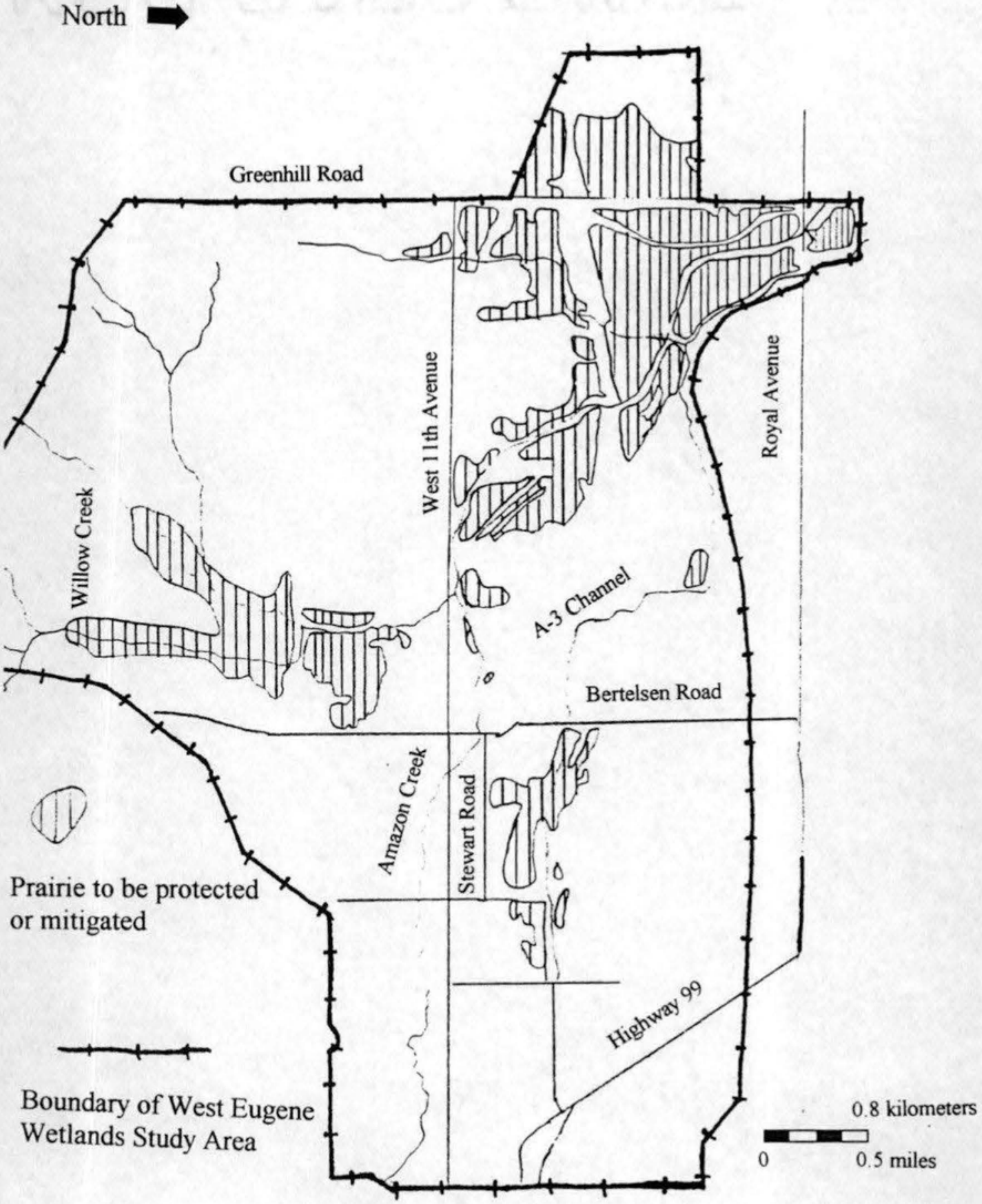

Figure 3. West Eugene Wetlands Study Area (adapted from Lane Council of Governments, 1992).

partnership between the Nature Conservancy, the BLM, and the City of Eugene (Lane Council of Governments, 1992). The Nature Conservancy's Willow Creek Preserve is included in the WEWSA. The BLM is in the process of acquiring land within the WEWSA and the adjacent Coyote Creek area. As the BLM has acquired parcels of land for the purpose of protecting wetlands, it has frequently acquired high-quality upland prairies in the same parcels (J. Beall, 1994, personal communication). Thus, the Clean Water Act may indirectly aid in the preservation of upland prairie habitat. The final holdings of the BLM may be in the range of 8 to 16 km^2 (2000-4000 acres) (J. Beall, 1994, personal communication). The City of Eugene has current land holdings within the WEWSA, and desires to increase its holdings to over 4 km^2 (1000 acres) by 1998 (Lane Council of Governments, 1992).

The West Eugene Wetlands Plan (WEWP) establishes three categories of wetlands: those to be protected, those to be mitigated, and those to be developed. The areas to be protected or mitigated are in three clumps, at Stewart Road, at Willow Creek, and in the largest clump around the connection of Amazon Creek and the A-3 Channel (See Figure 3.) The WEWP also led to the formation of a wetlands mitigation bank.

There are significant concerns about the spatial arrangement of areas to be preserved under the WEWP. Connections between major parcels are not adequately emphasized. The Willow Creek site is about 0.8 km (0.5 miles) from the edge of the lower Amazon site. Willow Creek forms a natural corridor for migration. The sites are separated by West Eleventh Avenue, a major road. Of greater concern is the Stewart Road clump. The wetlands to be preserved at this site are less than 0.4 km^2 (100 acres), and are about 2 km (1.2 miles) from the Amazon-A-3 clump (see Figure 3). The only hydrologic connection is the long, degraded, and polluted A-3 Channel, and the sites are separated by three large roads. Migration between these clumps would be perilous or impossible for all wetland species except perhaps birds and flying insects.

An overall conservation plan for the wet prairie must emphasize connections, corridors, and large areas of contiguous habitat. The three clumps in the WEWSA would benefit from greater connectivity. For example, the Stewart Road clump could be linked more closely to the lower Amazon clump if the area just northwest of the corner of Stewart Road and Bertelsen Road were protected and enhanced, and if large culverts or bridges were installed to assist migration across Bertelsen Road and two other major roads between the clumps (See Figure 3.) Connections are also critical between the WEW and Fern Ridge Reservoir. The Amazon Creek enters Fern Ridge Reservoir through an artificial channel dug by the ACOE, which could provide a corridor between the two large preserves. (See Figure 2.) This section of Amazon Creek could be enhanced, possibly by detaining some water to create a wetland "stepping stone" between the sites. The ACOE is considering various options of restoring Amazon Creek above the reservoir (United States Army Corps of Engineers, 1993).

Restoration of degraded sites is also a priority in this area, since there are no pristine wet prairie sites remaining. Restoration will involve restoring the original hydrologic regime and the native vegetation. In many cases, filling ditches dug by farmers is all that is required to re-create the original hydrology (Galatowitsch and van der Valk, 1994). In other cases, dikes and levees must be broken or removed. The

ACOE is planning to do just that on a section of the Amazon in the western part of the WEWSA (United States Army Corps of Engineers, 1993). Large portions of the wet prairie sites in the WEWSA are intended for mitigation, in which a company or agency funds the restoration of degraded wetlands in exchange for the permission to dredge or fill wetlands at another site. Mitigation has already begun in the WEWSA.

The first wet prairie mitigation in the WEWSA involved a 16-hectare (40-acre) old field. The site was subjected to herbicides, prescribed burns and tilling in order to decrease the seedbank. Then, a mixture of 15 native seeds were sown. By the second season, the native *D. cespitosa* dominated the site, and eight other natives of the 15 seeded were located (Wilson, 1994).

Northern Willamette Valley Prairie Protection Efforts

In Portland, 800 hectares (1975 acres) of wetlands near the St. John's Landfill have been declared an urban natural area. As a part of the closing of this landfill, Portland's Metropolitan Services District developed a plan to restore native wet prairie species. Several experimental techniques are being implemented to reduce exotic species, including soil tilling, herbicide application, solarization (using clear plastic sheeting to heat the soil like a greenhouse in order to destroy the seed bank), pH manipulation, mowing, and burning. Native species have been planted on the site, but it is too early to know how successful the planting has been (Wilson, 1995). Also in Portland, a wet prairie is being restored along the Willamette River Greenway. This 0.8-hectare (2-acre) site, called Butterfly Park, is being restored by the City of Portland Park

Bureau. The site was deep-tilled, then subjected to hand-weeding and spot herbicide application, and finally covered with plastic sheeting for solarization. Afterwards, the first grass seeds and seedlings were re-introduced to the site. Plans call for the eventual planting of four grasses (*Bromus carinatus*, *Elymus glaucus*, *Festuca rubra* var. *rubra*, and *F. idahoensis*), and 32 forbs (Wilson, 1995).

Prairie restoration efforts benefit from networking and partnerships. The West Eugene Wetlands is an example of such a partnership, involving the BLM, the City of Eugene, and the Nature Conservancy. Another important partnership is the Willamette Valley Natural Areas Network, whose members include representatives of the BLM, the Nature Conservancy, the ACOE, Oregon State University, and the U. S. Fish and Wildlife Service. One specific goal of the network is to "restore and protect native habitats, primarily grasslands," and another goal is to increase support for prescribed burning, a management tool which can be controversial (Wilson, *et al.*, 1995).

Upland prairie restoration efforts lag behind the wet prairie restoration projects. This is due partly to the Clean Water Act of 1972, which contains strong measures to preserve wetland areas. Existing wetlands are required to be maintained or else other wetlands are to be created or enhanced whenever existing wetlands are degraded by development (Want, 1990). Also, the listing of *L. bradshawii* as a federal endangered species has encouraged research into Willamette Valley wet prairies (Kaye, *et al.*, 1994). Cheryl Schultz, a researcher from the University of Washington, has begun the most extensive effort to compare restoration techniques for upland prairie habitat.

Upland prairie is the habitat of *Icaricia icariodes fenderi*, Fender's blue butterfly.

This insect requires a specific host plant, *Lupinus sulphureus kincaidii*, Kincaid's lupine, for its larval food source. *L. sulphureus kincaidii* is restricted to upland prairie, and exists in only a few sites in the Willamette Valley. The rare status of this plant (a Candidate 2 species), and the subsequent rarity of the butterfly, are stimulating research into methods of restoring upland prairie.

Schultz is conducting research into the effectiveness of various soil preparation techniques and planting ratios aimed at restoring a native plant community in areas that have been degraded by agricultural uses. She is working in the West Eugene Wetlands area, at sites owned by the Nature Conservancy and the BLM (Schultz, 1995b). Experimental plots were established at three sites. Soil preparation techniques include tilling, solarization, reverse fertilization, and no-till (control). In experimental plots, seeds of eleven native plants were sown and one species (*Camassia quamash*) was planted as a bulb. The mix included four grasses, *L. sulphureus kincaidii*, and four species adult *I. icariodes fenderi* individuals use as nectar sources. Seed mixes were done at two different ratios of grasses to forbs. Plots will be monitored for the next four to five years to determine the effectiveness of different treatments. The goal of the project is to develop possible methods for restoring large areas for *I. icariodes fenderi* habitat (Schultz, 1995b).

CHAPTER III

STUDY ORGANISMS AND STUDY AREA

Both *L. bradshawii* and *E. decumbens* are endemic to the Willamette Valley. They have been reduced to less than 20 sub-populations each, and both exist in large numbers at only a handful of sub-populations. As a result of their rarity, these plants have been the focus of botanical description and ecological research over the past 15 years. Much of this research has taken place at Fern Ridge Reservoir, an area west of Eugene, Oregon, managed by the Army Corps of Engineers. (See the section Prairie Preservation Attempts.) Below are descriptions of the study species, their ecology, research results, and a description of the site at Fern Ridge Reservoir where this research took place.

Biology of *L. bradshawii*

Description of *L. bradshawii*

Lomatium bradshawii (Rose ex Math.) Math. and Const. is known to occur only in Oregon's Willamette Valley. It is a member of the parsley family (Apiaceae or Umbelliferae). Common names are Bradshaw's lomatium or Bradshaw's desert-parsley. It was first described by Nelson, who collected a specimen near Salem, Oregon (Kagan, 1980). No collections were made between 1941 and 1969, and the species was suspected to be extinct (Parenti, *et al.*, 1993). However, by 1980, eight populations had been located, and by 1994, sixteen populations were known to exist (Kaye, *et al.*, 1994). *L. bradshawii* is the only federally-listed endangered plant species in the Willamette Valley.

The plant is a perennial herb which generally grows 20 to 40 cm tall. Mature plants have 2 to 6 well-dissected leaves 10 to 20 cm long. Segments of the dissected leaves may be 2 to 12 mm long. Leaves tend to extend further vertically than horizontally. Reproduction in *L. bradshawii* is exclusively through seed production rather than vegetative spread. Therefore, successful flowering, pollination and seed production is mandatory for the propagation of the species.

L. bradshawii produces small, yellow flowers in compact inflorescences called umbels. Plants have 0 to 3 umbels (Kagan, 1980). An umbel is an "inflorescence with a very short axis and more elongate [flower stalks] which seem to arise from a common point" (Hitchcock and Cronquist, 1973, p. xix) which are divided into umbellets less than 1 cm in diameter, with petals about 1 mm long. Each umbel may have 5 to 14 umbellets. Beneath the flowers are sets of three bracts (Kagan, 1980; Wilson, *et al.*, 1993).

There are two types of flowers, male and hermaphroditic, which are part of a reproductive system that promotes out-crossing (the mating of two plants). Male flowers have only stamens, and produce only pollen. Hermaphroditic flowers have both stamens and pistils, and produce both pollen and seeds. Over 90% of the flowers are male (Kagan, 1980). The first flowers a plant produces are almost exclusively male, and the percentage of hermaphroditic flowers increases in later flowers, although they never outnumber the male flowers. Kagan (1980) found that no plants contained hermaphroditic flowers at the beginning of the blooming season and 21.3% of the plants contained hermaphroditic flowers one month later. He also estimated that male flowers outnumber hermaphroditic flowers by 4 to 1 in the umbels containing both types of flowers. Hermaphroditic flowers are usually on the outer umbellets of an umbel, and usually on the outer edges of these umbellets (Kaye, 1992). These outer flowers always bloom first, meaning that the maturity of the hermaphroditic flowers occurs at a different time than the maturity of the male flowers of the same plant. This is called protogyny, and promotes out-crossing. Kagan (1980) determined that the plant is self-compatible, but the protogyny means that self-fertilization is likely to occur only after hermaphroditic flowers have been through most of their blooming cycle without receiving pollen from another source. *L. bradshawii* is incapable of producing seeds without pollinating insects (Kaye and Kirkland, 1994).

L. bradshawii produces a large, oblong seed, 8 to 13 mm long and 5 to 7 mm wide (Hitchcock and Cronquist, 1974; personal observation). From 1 to 20 seeds may form at the site of each umbellet. Seeds are arranged in pairs that sit back to back until ready to drop from the plant. Most pairs of seeds curl apart from each other, but some pairs do drop together (personal observation).

Seeds are produced in May, June, and July. The seeds sit in clumps called pedicels. Pedicels may be 15 to 40 cm high (personal observation). Seeds are passively released from the pedicel, and generally fall within one meter of the parent plant. There is no evidence that animal vectors are significant in moving the seeds from their original landing site, and the size and shape of the seeds makes it unlikely that wind would move them. However, the seeds are buoyant, and water movement could be a significant vector for *L. bradshawii* (Wilson, *et al.*, 1993).

This plant is one of the earlier perennials in its habitat. Leaves are visible as early as February. Peak blooming occurs in April and May. Seeds appear from late May to early July (Kagan, 1980). Seeds may stay on the plant until October or November (personal observation).

L. bradshawii is associated with *Deschampsia cespitosa*, tufted hair-grass. This grass is a dominant species in Willamette Valley wet prairie. *D. cespitosa* forms small hummocks, with diameters of approximately 30 cm and heights of 20 to 40 cm. These mounds allow the roots of *D. cespitosa* to be aerated. *L. bradshawii* tends to grow on these hummocks, although it also grows in the low areas between the hummocks. It also seems to do better where the *D. cespitosa* population has begun to senesce, possibly because there is less competition for sunlight (Kagan, 1980). *L. bradshawii* is attacked by a Chytridiomycete fungus, Ceropidae (spittle bugs), and Aphididae (aphids) (Kagan, 1980).

Research on *L. bradshawii*

As a part of the attempts to restore prairies of the Willamette Valley and to benefit the rare native plants, controlled burning has been evaluated at several sites in the Willamette Valley (Pendergrass, 1995). Studies done at the same Fisher Butte site that is the focus of this study have evaluated the response of *L. bradshawii* to prescribed fires.

Parts of Fisher Butte were burned in 1988 and again in 1989. By 1990, seed production had increased by a factor of 7. *L. bradshawii* plants at Fisher Butte also seemed to benefit from the burns in terms of umbel production, umbellet production, and crown size. At another site, effects were similar, but less pronounced. Also, mortality was highest among unburned plants at both sites (10% and 14.9%) and lowest among the once-burned plants (4.1% and 3.6%) (Connelly and Kauffman, 1991).

Kagan (1980) observed infrequent insect visitors to *L. bradshawii* at four sites near Eugene. He saw two potential pollinators, an *Andrena* species of solitary bee and a wasp-mimic Dipteran. Kaye (1992) observed more insects and more insect species (25) visiting the plants. He noted 10 species that he found to be carrying pollen and that seemed by their behavior to be effective pollinators. These included solitary bees (a *Melanostoma* species, a Tenthredinidae species, and two *Andrena* species), wasps (Ichneumonidae species), flies (*Mesograpta marginata, Paragus* species, *Sphaerophoria* species, and *Xylota* species), and beetles (*Lebia moesta*). Kaye and Kirkland (1994) observed 38 insect species visiting the flowers over a three-year period, including solitary bees (Andrena species), muscoid flies, and syrphid flies.

Because *L. bradshawii* flowers so early in the spring, insect pollinator availability is limited. Muscoid flies and syrphid flies may be important to this plant, despite being inefficient pollinators, because they can be active in cold and wet weather (Cole, 1969), which is often the dominant weather during *L. bradshawii* blooming season. The large variety of species observed suggests that the plant is not highly vulnerable to population fluctuations among one insect species (Kaye, 1992). No observation of insect pollinators of *L. bradshawii* has found a single dominant species. (The observation of pollinators described in this research does identify a pollinator that occurred in 44% of the tracked insects. See the section called Lomatium Pollinators.)

Recovery Plan for *L. bradshawii*

Parenti and colleagues (1993) developed a recovery plan for the plant. They identify habitat loss as the major factor threatening the species. Also, limited fecundity is cited as a significant concern, and is suspected to be due to inbreeding. Experimental cross-breeding is recommended, but the authors caution that populations may have site-specific adaptations that could be weakened by cross-breeding. According to the plan, down-listing (from endangered to threatened) could occur when 10 viable populations exist, divided among 4 geographic areas in the Willamette Valley. A viable population is defined by the recovery plan as a population on 20 or more contiguous acres (8.09 hectares) of secured property (government or conservation agency ownership or conservation easement). Also, the population must have greater than 2000 flowering plants, and a population structure that allows a population to increase or remain stable. Furthermore, active management of these populations is considered critical, mainly due to potential invasion of wet prairies by woody species. Prescribed burning is recommended as a management tool. Currently, there are three sites that meet the recovery plan criteria for viable populations, at the West Eugene Wetlands (including the Nature Conservancy's Willow Creek Preserve) near Eugene, Oregon, the Army Corps of Engineers Fern Ridge Reservoir, also near Eugene, and the William Finley National

Wildlife Refuge near Corvallis, Oregon. (See the previous section Southern Willamette Valley Prairie Protection Efforts for more details about these areas.)

Biology of *E. decumbens*

Erigeron decumbens Nutt. var *decumbens*, also known as the Willamette daisy, Pacific fleabane, or meadow erigeron, is found only in the Willamette Valley. It was not collected between 1934 and 1980, and was considered extinct until rediscovered at Willow Creek near Eugene in 1980 by James Kagan (Clark, *et al.*, 1993). It is currently a Category 1 Candidate for the Federal Endangered Species list, and is listed as endangered on the Oregon Endangered Species list. It has been proposed for endangered status on the federal list, but a congressional action to suspend new listings has halted its progress (Wald, 1996). *E. decumbens* is a member of the Asteraceae family (Hitchcock and Cronquist, 1974). Eighteen populations of *E. decumbens* are now known (Clark, *et al.*, 1993).

Significant taxonomic changes have occurred recently in the *E. decumbens* genus. Cronquist (1947) considered Willamette Valley specimens of *E. decumbens* to be the same species as plants growing in southern Oregon and northern California. He labeled the Willamette Valley specimens as subspecies *decumbens* and the southern specimens as subspecies *robustior*. More recently, *decumbens* var. *robustior* has been reduced to two counties in California, and southern Oregon Erigeron specimens have been re-classified as *Erigeron eatonii* var. *plantagineus* (Strother and Ferlatte, 1988). Thus, the Willamette Valley plants might now be considered a more separate and distinct population, both genetically and geographically. However, the parallel morphology within the Erigeron genus complicate taxonomy of the group (Nesom, 1989). It has also been suggested that *E. eatonii*, *E. jonesii*, *E. lassenianus*, *E. nevadincola*, and *E. sonnei* are all a single species (Strother and Ferlatte, 1988).

E. decumbens is a perennial herb 20 to 60 cm tall. Stems may be erect or decumbent at the base and curving upward. Leaves are simple and narrow, linear to oblanceolate, 5 to 12 cm long and 3-6 mm wide. Flowering stems have 2 to 5 inflorescences. Each infloresence has 25 to 50 rays, pinkish to blue, that fade to white. Flowers resemble daisies. The plant blooms in June and July. It produces and drops seeds in July and August. Seeds are small, with a pappus (Clark, *et al.*, 1993; Strother and Ferlatte, 1988). More than 150 seeds are produced per flower (Clark, *et al.*, 1993). In field observations, the total number of seeds per plant ranges from 486 to 1770 (Ingersoll, *et al.*, 1995).

E. decumbens grows in wet prairies and upland prairies. In wet prairie areas, it often grows in association with *D. cespitosa* populations, but tends to avoid the densest concentration of these grasses. It prefers the driest of habitats in which *D. cespitosa* can grow, and thus where it is sparse (Clark, *et al.*, 1993). It can tolerate soils that are seasonally flooded (personal observation). In upland prairies, *E. decumbens* grows in communities dominated by *Festuca rubra* (red fescue), *Bromus carinatus* (California brome), and *Elymus glaucus* (blue wildrye) (Clark, *et al.*, 1993). Encroachment by woody vegetation apparently causes *E. decumbens* to retreat (Clark, *et al.*, 1993), although one population at Willow Creek has increased in the presence of woody vegetation (Pearl, 1995, personal communication). There are no known diseases or predators of *E. decumbens* (Clark, *et al.*, 1993).

Research on *E. decumbens*

As with *L. bradshawii*, *E. decumbens* has been evaluated to determine its response to controlled burning. The Fisher Butte site was partially burned in 1988 and 1989, resulting in some areas that were burned twice, some that were burned once, and some that were not burned at all. Although *L. bradshawii* had a very positive response to prescribed fires, the response of *E. decumbens* was less clear. One year after the first fire, plant height and flowering was decreased. However, by 1990, height was similar between all three conditions and flower production by once-burned and twice-burned plants was greater than that of control plants. By 1990, crown growth was greater in once-burned and twice-burned plants than in control plants. Mortality was greater in 1989 and 1990 for burned plants than for unburned plants, but density of plants increased greatly in burned patches as compared to unburned patches. Most of this increase was in vegetative plants, suggesting that reproduction benefited from the burns (Connelly and Kauffman, 1991). Because some of the measurements of the control plants varied greatly from year to year, it is suggested that more study is needed to determine which of these differences are due to the burn treatments and which are due to normal annual variability in plant vigor.

E. decumbens tends to grow in clumps of genetically identical ramets. Its distribution at most sites is patchy, with scattered clumps of plants (Clark, *et al.*, 1993).

Thus, it is difficult to make accurate counts of populations. (For the purposes of this research, the population and density estimates of Clark and her colleagues (1993) will be used.)

Clark *et al.* (1993) observed several insect species apparently acting as pollinators of *E. decumbens*. These included four Hymenopterans (*Ceratina* sp., *Megachile* sp., *Nomada* sp., and *Halictus ligatus*), two Coleopterans (*Meligethes nigrescens* and *Acanthoscelides pauperculus*), and two Dipterans (*Toxomerus marginata* and *Tachina* species). An earlier status report on the species noted butterflies, ground nesting bees, bumblebees, flies, and honeybees on flowers (Kagan and Yamamoto, 1987).

The 18 known populations of *E. decumbens* all occur in the Willamette Valley. Of the three largest, Baskett Slough National Wildlife Refuge contains 315 flowering clumps in two separate populations, Fern Ridge Research Natural Area contains approximately 2600 flowering clumps in four separate populations, and Willow Creek contains approximately 2080 plants. The largest population at Baskett Slough contains 370 clumps, and the largest two populations at Fern Ridge contain 1500 and 1000 clumps. Baskett Slough and Fern Ridge are both federally-managed sites, and Willow Creek is owned by the Nature Conservancy.

Two status reports have been written for *E. decumbens* (Kagan and Yamamoto, 1987; Clark, *et al.*, 1993). Both recommend that the plant be listed as endangered under the federal Endangered Species Act. Habitat loss and fragmentation is considered the main reason for the decline of *E. decumbens* from historical population levels. Invasion of prairies by woody species and exotics is also a major threat to the species (Clark, *et* *al.*, 1993). Clark and her colleagues recommend control of invasive species in prairie habitats, coordination with local highway departments for the management of roadside populations, and efforts to continue prescribed burning as a management tool.

A study of the reproduction of *E. decumbens* has examined seed viability, germination requirements, phenology of seed germination, and techniques of propagation (Clark, *et al.*, 1995). Less than 20% of seeds were found to be robust, which could be due to a lack of pollinators or resource deficiencies during seed growth. Of those robust seeds, around 60% are viable. The highest percent germination obtained by Clark and her colleagues was 83%. They planted robust seeds in September of 1994, and again in January of 1995, and obtained seed germination in April of 1995 (D. Clark, 1996, personal communication). Finally, transplanting seedlings proved to be difficult. In two trials, using 121 seeds, only one seedling survived (Clark, *et al.*, 1995).

Experiments with vegetative propagation were more successful than the seed germination tests. Of cuttings that included rhizomes, 33% survived for 26 weeks, the duration of the trial (Clark, *et al.*, 1995). This research suggests that, unless improvements are made to seed preparation techniques, vegetative propagation would be a more successful tool than seeding to create new *E. decumbens* populations or add new plants to existing populations. Furthermore, the results indicate that *E. decumbens* might rely more on vegetative spread to reproduce than it does on seed dispersal.

Study Site Description

Fern Ridge Reservoir is located 7 kilometers (4.3 miles) west of Eugene, Oregon, on Highway 126. The reservoir was created by the Army Corps of Engineers (ACOE) in 1941, through the construction of a dam across the Long Tom River. The ACOE now controls 52 km^2 (12,780 acres) of land in the area, approximately three-quarters of which is open water, depending on the water level (R. Hayes, 1996, personal communication). This land contains valuable wet prairie and upland prairie sites (Wilson, *et al.*, 1993). Fisher Butte is one of eighteen management units under ACOE control at the Fern Ridge Reservoir. It is 5.78 km^2 (1428 acres) in size. Of this area, over 300,000 m^2 (76 acres) is the Fern Ridge Natural Research Area, the only Natural Research Area in the country under the control of the ACOE (R. Hayes, 1996, personal communication). The Research Natural Area contains two wetland plant communities. To the south is a *Deschampsia cespitosa-Danthonia californica* community. To the north is a slightly wetter *Rosa nutkana-Deschampsia cespitosa-Juncus nevadensis* community (Wilson, *et al.*, 1993). (See Figure 4.) This Research Natural Area has been the site of much research, as it is one of the best-preserved wet prairies of the Willamette Valley. The Fisher Butte Management Unit contains large populations of both study species.

There are two soil types under the Fisher Butte Management Unit. About 60% of the unit is Natroy silty clay loam, and about 40% is Dayton silt loam, clay substratum (Soil Conservation Service, 1987). Both of these soils are deep, poorly drained soils formed of alluvium on terraces (Soil Conservation Service, 1987).

At the Fisher Butte Management Unit, the density of *L. bradshawii* was measured in a representative patch. Due to the sensitive status of the species, their precise location within the management unit is not provided in this document. (Those

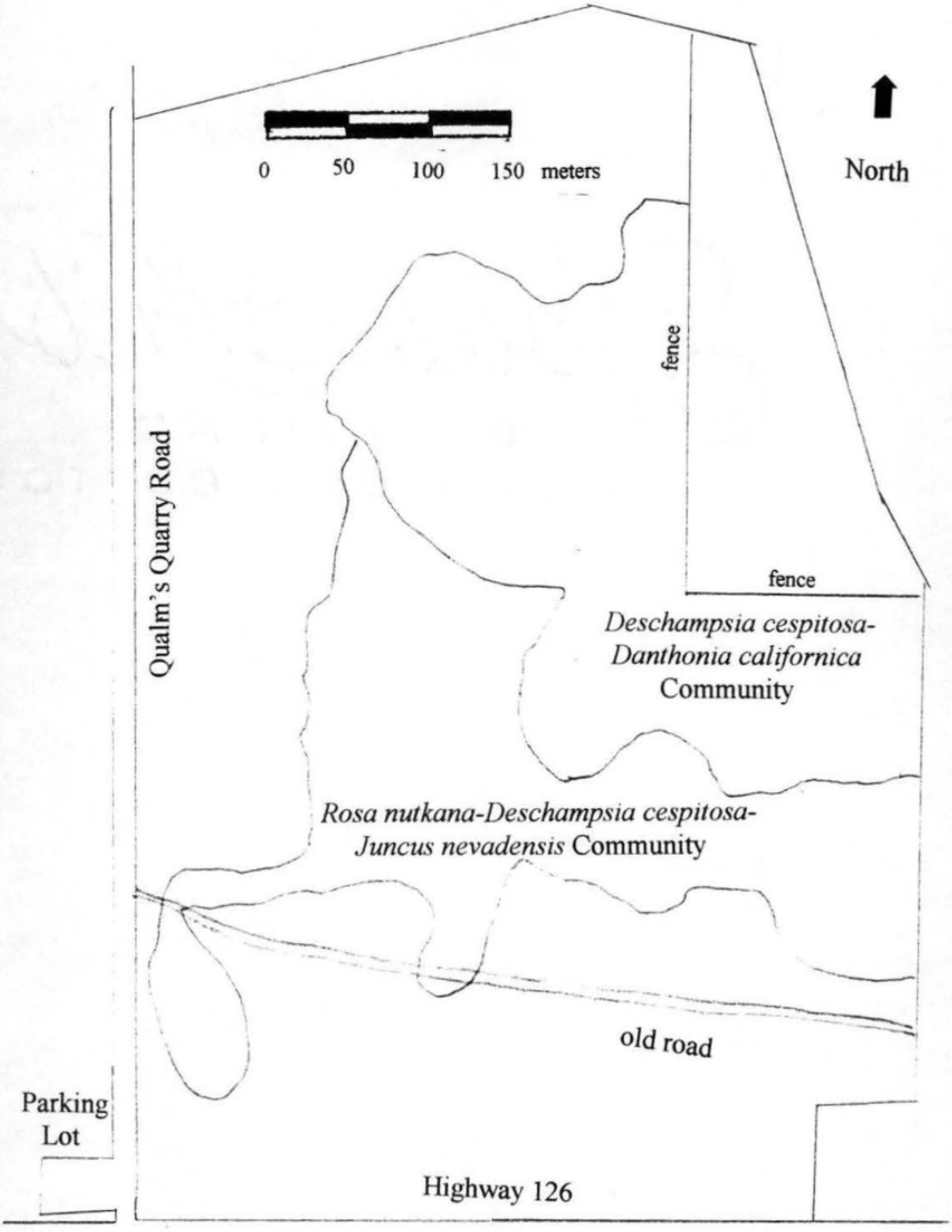

Figure 4. Fisher Butte study area (adapted from Wilson, *et al.*, 1993).

interested in the precise locations of the study areas can contact the ACOE at Fern Ridge Reservoir.)

E. decumbens grows in both wet prairie and upland prairie. In order to determine whether the different ecosystems would create different reproductive variables, one field day included observations at an upland prairie *E. decumbens* site in the Nature Conservancy's Willow Creek Preserve. This area is located in west Eugene, near Eighteenth Avenue and Bertelsen Road. The Willow Creek Preserve contains two soil types. Approximately 80% of the soil is Natroy silty clay loam, and approximately 20% is Steiwer loam. The area of the Willow Creek Preserve in which the observations took place contains Steiwer loam, a moderately deep soil formed of colluvium on low foothills (Soil Conservation Service, 1987).

CHAPTER IV

MATHEMATICAL MODELS

L. bradshawii and *E. decumbens* both exist in small isolated populations. Populations in these conditions may experience difficulty in reproduction due to inbreeding. The concept of a neighborhood has been developed to measure the actual, rather than theoretical, limits to sexual reproduction faced by small populations. Measurement of neighborhoods is based on the dispersal of offspring from their parents. Neighborhoods of plants are made easier to study because plants are sedentary, but are made more complicated because plants disperse genes in two packages, pollen and seeds. The formulae used to estimate neighborhoods have changed in the literature over the past 25 years of research, and that evolution is described below, along with the efforts made in this research to control for what is probably the largest unknown variable in research of pollen and seed dispersal, pollen carryover.

When a plant is insect-pollinated, pollen carryover may occur, and is extremely difficult to measure without some direct examination of the genetic material of offspring. Pollen carryover refers to the potential for an insect visiting a series of flowers to take pollen from the first flower, move it beyond the second flower, and deposit it at some flower later in the sequence. Due to the impossibility of observing such actions in the field, this research employed models to estimate the extent of pollen carryover, and to show the impact that such carryover would have on neighborhood measures. The models used to make these calculations are also described below.

Neighborhood Concept

A population of a species is defined as a subset of the entire number of that species which is genetically connected (Crawford, 1984a). In sexually reproducing species, a population is a set of individuals that has a possibility of breeding. Animals of the same species living on different islands may be unable to cross the water between the islands. In that case, a set of animals on an island would be a different population from a set of animals on a nearby island. In plants, the lack of mobility of sexually mature individuals generally means that there are more barriers to breeding. Rivers, soil types, roads, and agricultural lands can act to separate plant populations. Thus, a nature preserve that provides unrestricted movement for animal species could be sub-divided into several distinct populations for plant species. It is crucial information for resource managers to know the possibilities of gene flow between plant populations. For sexually reproducing plants, gene flow depends on the dispersal of pollen and the dispersal of seeds.

In an ideal population, mating occurs completely at random. However, populations in the real world do not generally meet the criteria of random or unconstrained mating. Therefore, in terms of genetics, a population is effectively smaller than in terms of actual individuals (Wright, 1969,1976). Wright (1931) developed the concept of the effective size of a population, N_e. This is "the number of breeding individuals in an ideal population that would show the same dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration" (Crawford, 1984a, p. 142.)

Wright (1946) also developed the concept of a neighborhood, which is "the area from which the parents of central individuals may be treated as if drawn at random" (Wright, 1969, p. 291). Neighborhood effective size equals neighborhood area multiplied by density:

$$N_e = A * \text{density}$$

Individuals are considered to be distributed at some uniform density throughout an area. The size of the area depends on the variance of dispersal distances of offspring (Crawford, 1984a). The general formula for neighborhood area, A, is:

$$A = 4(\pi)(\sigma^2)$$

where σ^2 = variance in distance offspring are dispersed from their parents.

For plants, dispersal of both pollen and seed are components of the total dispersal of genetic material from the parent to the offspring. Therefore, the dispersal of pollen, σ_p^2 and the dispersal of seeds, σ_s^2, are separated in the equation:

$$A = 4(\pi)(\sigma_p^2 + \sigma_s^2)$$

There have been several renditions of this formula for a neighborhood. Early papers used the formula exactly as above (Levin and Kerster, 1968). Later, these same authors modified the formula by dividing the variances by 2 to find the average of pollen dispersal and seed dispersal (Levin, *et al.*, 1971). Still later, they added a correction factor to account for the fact that pollen is haploid and seeds are diploid (Levin and Kerster, 1974):

$$A = 4(\pi)(0.5)[(0.5)\sigma_p^2 + \sigma_s^2]$$

Crawford (1984b) explained that all three of these formulae are incorrect. Pollen dispersal is the male gamete dispersal, and seed dispersal is the offspring dispersal. Pollen dispersal only moves the male half of the genes of the offspring, i.e., is haploid. Seed dispersal moves the female half of the genes, and the male half again. The variance in pollen dispersal must be weighted by a factor of 0.5 because it only involves half of the genetic material of the future offspring (Crawford, 1984b):

$$A = 4(\pi)[(\sigma_p^2/2) + \sigma_s^2].$$

The equation may be further modified by consideration of self-fertilization. Levin and Kerster (1971) proposed the addition of a self-fertilization factor, t, into the equation, where (1 - t) is the proportion of offspring produced by self-fertilization above what would be expected under random mating. They rewrote the equation as:

$$A = 4(\pi)t[(\sigma_p^2/2) + \sigma_s^2].$$

Crawford (1984a) pointed out that this equation would result in a neighborhood area of zero where there is no out-crossing, which does not account for seed dispersal. He therefore rewrote the equation as:

$$A = 4(\pi)[(t\sigma_p^2/2) + \sigma_s^2].$$

For the species being examined in this research, however, this term will not be included. *L. bradshawii* is self-compatible, but has a reproductive system (protogyny) which strongly favors out-crossing. Thus, *t* would likely be nearly equal to one. For *E. decumbens*, no information is available on the rate of self-fertilization, so no estimate of *t* would be possible. For these reasons, this term will not be included in the formula.

Crawford (1984a) also suggested alterations to the equation to reflect kurtosis (the skewedness from a normal distribution) in the dispersals. Insect pollinators have been shown to have strong leptokurtosis in their flight distances (Levin and Kerster 1969, 1971, 1974), and wind-dispersed seeds have also been shown to have leptokurtic distributions (Levin and Kerster, 1974; Bateman, 1947). Since the leptokurtosis of pollen distribution is not linked to the leptokurtosis of seed distribution, two correction factors are needed, k_p and k_s (Crawford, 1984a). In order to simplify the equation, k was set equal to 4 for a normal distribution, and the numeral 4 that was in the equation is removed. This is the form in which the neighborhood area will be calculated for *L. bradshawii* and *E. decumbens*:

$$A = (\pi)[k_p\sigma_p^2/2) + k_s\sigma_s^2].$$

Wright (1969, corrected 1977) offered a method to calculate the values of the kurtosis correction factors. In this study, kurtosis was calculated for seed dispersal and for pollen dispersal separately for each pollinating insect. See Appendix for a description of the calculation of *k*.

Finally, it is assumed in this model that dispersal distributions are rotationally symmetric. In other words, the seed and pollen will tend to disperse in random directions from the parent plant. If the direction of the wind during the time of seed dispersal is not random, then the dispersal of the seeds may have a directional component. Seeds may disperse farther downwind than upwind. It is also assumed that insect flights were directionally random. During observation of insect flights, no directionality was noted.

In order to compute the neighborhood areas for the study species, variances were obtained for pollinator flight distances. The variances were computed using the unmodified distance measurements for all insects observed. Kurtosis correction factors were also computed using the same data set. See Table 4 for the results. The neighborhood areas obtained from these calculations were further modified by the results of models of pollen carryover. The section on Pollen Carryover below contains a description of the calculation of these correction factors.

Pollen Carryover

When an insect transports pollen from one flower to another, it is likely that some of the pollen will not be dislodged at the second flower, but will remain attached to the insect for some longer period of time, and could eventually arrive at some flower later in the sequence of the insects travels. This is called pollen carryover. Early researchers into pollen movement assumed that the amount of pollen carryover is small (Levin and Kerster, 1969; Frankie *et al.*, 1976). However, that assumption has been challenged by experiments indicating that pollinator behavior, flower anatomy alone, and the interaction between flower anatomy and pollinator anatomy may cause significant pollen carryover. Studies that have compared pollen dispersal as estimated by pollinator flights with pollen dispersal as measured by gene flow have found that pollinator flight distances may underestimate actual pollen movement (Fenster, 1991; Broyles and Wyatt, 1991; Schaal, 1980).

Several studies have examined *Bombus occidentalis* bees pollinating *Erythronium grandiflorum* (glacier lily). Larger initial loads of pollen decreased the amount of pollen carryover. The large loads of pollen may be more likely to fall from the bees' bodies or may increase the frequency with which the bees remove the pollen by grooming. The overall rate of pollen carryover was such that mean pollen transport was equal to 6.03 flowers (Thomson, *et al.*, 1986). Further studies of the same flower, with various *Bombus* species, noted that the bees removed a mean of 62.1% of the pollen from flowers they visited, then delivered a mean of 0.52% of the removed pollen to other flowers' stigmas. Mean transport distance of out-cross pollen was 3.08 meters, over 32 runs (Thomson and Thomson, 1989).

There is evidence that pollen carryover may be strongly influenced by flower shape, regardless of pollinator anatomy. If variation is greater in the positioning of anthers within a flower, then mean pollen transportation distance is greater as well (Lertzman, 1981, in Campbell and Waser, 1989). This hypothesis is born out by other experiments. Waser and Price (1984) found that carryover increased with floral variability in *Ipomopsis aggregata*, scarlet gilia.

Thomson and Plowright (1980) measured pollen carryover in three species of flowers, *Erythronium americanum*, *Clintonia borealis*, and *Diervilla lonicera*, using bumblebees of the genera *Bombus* and *Psithyrus* as pollinators. Within a sequence of floral visits, the bumblebees were introduced to a flower that either had natural dimorphism in pollen color from other flowers in the sequence or to one pollen-containing flower in a series of emasculated flowers. Unfortunately, their sample sizes were small, and the variability of pollen movement was large. In *E. americanum*, 20.5% of pollen was deposited on the first flower visited, 23.2% was deposited on the second flower visited, 7.9% was deposited on the third flower visited, 13.7% was deposited on the fourth flower visited, and 10.0% was deposited on the fifth flower visited. A total of 75.3% of pollen was deposited on the first five flowers. In one sequence, a bumblebee deposited three grains of the identified pollen on the 54th flower visited. However, no other grains were deposited later than 29 flowers after the initial pollen-containing flower. In *C. borealis*, 34.6% of pollen was deposited on the first flower visited, 15.2% on the second flower, 12.9% on the third flower, 8.3% on the fourth flower, and 16.4% on the fifth flower. A total of 87.4% was deposited on the first five flowers. No pollen was deposited later than 12 flowers after being picked up. In *D. lonicera* 40.1% of pollen was deposited on the first flower visited, 17.2% on the second flower, 9.8% on the third flower, 7.2% on the fourth flower, and 12.9% on the fifth flower. A total of 87.1% was deposited on the first five flowers. In all three flowers, the insects were not picking up new pollen, as they would in a natural setting. Also, the emasculation of the *C. borealis* and *D. lonicera* flowers reduced the applicability of these findings. The authors point out that subtle differences in flower structure, insect anatomy, and insect behavior have major influences on the rate of pollen carryover (Thomson and Plowright, 1980).

Broyles and Wyatt (1991) studied the pollination ecology of *Asclepias exaltata*, the poke milkweed, which is pollinated by four species of butterfly and an unidentified member of the *Bombus* genus of bees. They compared potential pollen dispersal based on pollinator observance with realized pollen dispersal based on genetic paternity analysis, and found significant differences. They assumed zero pollen carryover for their observations of pollinator movement. The mean for realized pollen dispersal was more than three times larger than the pollen dispersal that would be predicted by observation of the insect pollinators. Neighborhood area calculated by realized pollen dispersal was 159.6 m^2, while neighborhood area calculated by pollinator observation was 23.3 m^2. However, *A. exaltata* has a pollination system that requires precise placement of the pollen in order for the pollen to reach the stigmatic chamber. The butterflies observed by Broyles and Wyatt often exhibited behaviors that may have decreased the probability of a successful pollination on any given flower landing. If the pollinators had a higher probability of successful pollination on a given landing, the mean distance of pollen movement would be lessened. In fact, work on a similar species has yielded shorter pollen dispersal distances when the pollinating agent is a honey bee (Pleasants, 1991). Other research on the pollinating abilities of bees indicates that pollen dispersal distances via bees may be so restricted that genes may only migrate a few meters a year (Handel, 1983).

A study of *Carduus nutans*, musk thistle, which is a Composite, found indirect evidence that pollen carryover was significant (Smyth and Hamrick, 1987). In an artificial, evenly distributed population of plants, lower levels of pollen carryover would be positively correlated with a greater degree of kurtosis. Distributions of pollen were found to be not significantly different from normal.

No direct studies of pollen carryover were found that dealt with Composite plants. The defining characteristic of Composites is a large number of small flowers together on one flower head. The small size of individual flowers relative to the pollinators suggest that the flowers' anatomical structure should not be specialized as are the structures of *I. aggregata* and *A. exaltata*, described above. Schmitt (1980) studied the neighborhood size of five species of *Senecio* (ragwort), pollinated by both *Bombus* (bumblebees) and various butterflies. She pointed out that if pollinators visit several flowers per plant, this would tend to limit the effect of pollen carryover. She also examined the impact of differing behaviors of bees and butterflies. Schmitt found a mean neighborhood area of 2.19 m^2 with bumblebee pollination alone, and a mean neighborhood area of 211.57 m^2 with butterfly pollination alone.

Schmitt (1980) argued that pollen carryover should be greater with butterflies than with bees. There are three reasons for this. First, butterflies generally visit fewer flower heads per plant than bees do. Therefore, more of the pollen that is carried over will be deposited on another plant. Second, in a foraging bout, butterflies visit fewer plants than bees do. After a foraging bout, the butterflies may travel to a new patch. This would increase the distance of pollen movement by increasing the number of between-patch flights in a day. Finally, bees display repetitive visits to the same plants or patches of plants. This limits their ability to move pollen to new flowers. These differences make butterflies more effective as long-distance pollinators than are bees, and should cause butterfly-pollinated plants to have larger neighborhood areas than bee-pollinated plants (Schmitt, 1980).

Fenster (1991) examined the pollination of *Chamaecrista fasciculata*, the partridge pea, which is pollinated by bees, mostly *Bombus* species. He calculated a neighborhood area of 2.8 m^2 based on pollinator flights (assuming no carryover) and a neighborhood area of 9.6 m^2 based on gene flow.

Pollen Carryover in *L. bradshawii* and *E. decumbens*

Because both *L. bradshawii* and *E. decumbens* produce small flowers, variability in flower anatomy is not likely to create a large amount of pollen carryover. The effect of pollen carryover on neighborhood areas was estimated with two arbitrarily-set pollen deposition frequencies. These two carryover models are those that were used by Levin and Kerster (1969). In the high pollen carryover model, an insect landing on the second flower in a sequence deposited 50% of the pollen from the first flower. On the third flower, it deposited 25%, then 12.5%, 6.5% and 6% on the fourth, fifth, and sixth flowers, respectively. In the low pollen carryover model, an insect landing on the second flower in a sequence deposited 80% of the pollen from the first flower, then 15% and 5% on the third and fourth flowers, respectively. These models were compared to a no-carryover model, i.e., one in which the insect deposited 100% of its pollen load on the next flower it visits.

In order to calculate the neighborhood areas given some levels of pollen carryover, the data were re-organized. First, if a flight sequence began on a flower other than the study species, that stop was deleted. Then, all sequences less than six stops were eliminated. In the sequences remaining, all sequences of six stops were set as separate sequences. For example, if a sequence was observed of ABCDEFG, where each letter represents a separate flower stop, then this sequence was divided into ABCDEF, showing the movement of pollen from flower A, and BCDEFG, showing the movement of pollen from flower B. Within each sequence, stops at flowers of non-study species were recorded as stops where some pollen was lost, just as it would have been were the stop at the study species, but the distance of pollen movement was recorded as zero. Also, some sequences involved returns to the original flower (ABCACA, for example). For these stops, the distance of pollen movement was also recorded as zero. Finally, sequences that began on one of the study species flowers, but did not move any pollen to other flowers of the target species, were eliminated.

For the high pollen carryover model, the portions of pollen deposited were assumed to be 50% at flower two, 25% at flower three, 12.5% at flower four, 6.5% at flower five, and 6% at flower six. For the low pollen carryover model, the portions of pollen deposited were assumed to be 80% at flower two, 15% at flower three, and 5% at flower four. To reflect the total distance moved from the first flower, the percentages were multiplied by the sums of squares of the distances of each preceding flight in the sequence. The same sets of sequences were used to compute the high carryover model, the low carryover model, and a no carryover model, in which the variance was set equal to the variance of the distances moved on the first flights of the sequences. Therefore, the output of the carryover models was a set of variances for the high, low and no carryover models. These corrected variance values were then used to calculate the final estimates of neighborhood area.

The variances calculated using the sequence data set were used to obtain carryover correction factors. The correction factor for the no-carryover condition was 1. The correction factor for the low-carryover condition was obtained by dividing the low-carryover variance by the no-carryover variance. This produced a factor by which the variance changed from the no-carryover model to the low-carryover model. The same process created a correction factor for the high-carryover condition. These correction factors were then multiplied by the variance calculated for pollen (σ_p^2) using the raw data set, as described in the section Neighborhood Concept.

CHAPTER V

METHODOLOGY

In order to develop measurements of neighborhood area and size, seed and pollen dispersal distances, and density estimates were obtained for both study species. Pollen dispersal was measured indirectly in the field for both species by observation of movements of pollinating insects. Seed dispersal was measured directly in the field for *L. bradshawii*. For *E. decumbens*, seed dispersal was estimated using laboratory measurements of seed behavior combined with data from a local weather station. Density was measured directly in the field for *L. bradshawii*, and was taken from previous research on *E. decumbens*. The methods used to obtain this data are described below.

Pollen and Seed Dispersal Measurement

L. bradshawii Pollen Dispersal Measurement

Pollen dispersal was measured in the spring of 1995. Initially, a technique was attempted using fluorescent dye to mimic pollen movement. A powdered dye was applied to the flowers in such a way that insects landing on the flowers might pick up the dye and move it to other flowers. This technique has been effective in other pollination studies (Campbell and Waser, 1989; Murawski, 1987; Palmer, *et al.*, 1988; Parra, *et al.*, 1983). Two different colors of dye were used and were applied to flowers at varying intensities. The dye was applied in the morning, and on the evening of the same day, flowers in the vicinity of the dyed flowers were examined for the presence of dye. This dyeing was conducted on two occasions, and observations took place on four occasions, but no dye was ever observed any flowers except on those where it was originally applied.

The second method of pollen dispersal measurement was direct observation of pollinating insects. This observation took place on eight days between April 22, 1995 and May 8, 1995. The observer established a position approximately one meter from a patch of blooming *L. bradshawii* such that the shadow of the observer did not cover the flowers. The observer then stood still for approximately two minutes to minimize any effects of movement on insect behavior. (In some cases, the waiting period was omitted, as insects were observed while moving through the patch, and approaches could be made that did not appear to influence insect behavior.) Insects were tracked as they moved from flower to flower. Small numbered wooden sticks were used to mark flowers that insects had visited, unless insect proximity prohibited such movement. In those cases, flower positions were memorized, sometimes with the aid of simple maps sketched of flower patches. Once the insect had departed, distances between flowers were measured to the nearest centimeter. Insect stops were recorded at flowers of other species, as were stops on vegetation, and stops that involved preening that appeared to remove most of the pollen. *L. bradshawii* flowers were numbered for each insect's observed path, and movements between flowers of different individual plants were distinguished from movements among flowers of the same plant. Letter codes were used to describe the ends of flight sequences. Insects that were lost by the observed were coded as "D" for disappeared. Insects that moved out of sight or further than the observer could travel without potentially stepping on a study plant were coded as "A" for flying away. Some insect flight sequences were given no letter code, as the observation of these insects was abandoned because the insects were not making further flights quickly. Flights that were coded A later had an additional flight distance added to the flight sequence to approximate the distance of the flight away from the observer. For *L. bradshawii* pollinators, a distance of 4 meters was given to each flight coded as A by the bees of the Andrena species, and a distance of one meter was given to each A flight by all other insects. These numbers were estimates based on observations of the insects' behavior. (See the section called Lomatium Pollinators and Table 2.) The data with this modification were used to calculate variance in pollen distribution, pollen carryover, and pollen distribution kurtosis.

L. bradshawii Seed Dispersal Measurement

L. bradshawii seed dispersal was measured in the field using fluorescent dye (Radiant Dye Corp.). *L. bradshawii* plants were selected at random using the following method: A transect was established running north and south through the Fisher Butte site. At five meter intervals along the transect, a metal flagging stake was twirled in the air. Five steps were taken in the direction the stake pointed. From that point, the stake was twirled again, and five steps were taken again. The nearest plant that had at least twelve seeds was then selected. This procedure was done twice at each five-meter interval, with two colors of dye being used. A total of 18 plants, containing 620 seeds, were marked. Dye in powder form was applied to all seeds of a selected plant. Dye was applied using large-gauge hypodermic needles to release a cloud of dye above the seeds. The dye initially covered the seeds, but within a few days of application, the dye was reduced to small amounts in the crevices of the seeds. Rainfall caused a reduction in the amount of dye, so the dye was reapplied after rainstorms. The plants were marked with metallic flags near each one. The number of seeds at each seed-head was recorded, and the presence of small, probably unfertile seeds was also noted. Regular checks were made on the marked plants. When the plant was observed to have lost seeds since the previous check, the ground around the plant was examined for dyed seeds. When dyed seeds were located, the distance from the seed to the main stem at the ground was measured to the nearest centimeter. The furthest a seed was ever discovered from the parent plant was 0.48 m, and the distance between plants dyed the same color was at least 5 m, so it can be assumed that the dyed seeds came from the nearest plant with similar dye color.

E. decumbens Pollen Dispersal Measurement

The first attempt to measure *E. decumbens* pollen dispersal employed the same technique as the first attempt to measure *L. bradshawii* pollen. Fluorescent dye was applied to *E. decumbens* flowers in the same manner as it had been applied to *L. bradshawii* flowers. Again, despite repeated attempts to locate dye that had moved from one flower to another, none was discovered. *E. decumbens* pollen dispersal was then observed directly in the same manner as *L. bradshawii* pollen dispersal. Observations occurred on six days between June 23, 1995 and July 14, 1995 at Fisher Butte, and on one day, July 4, 1995, at Willow Creek. As for *L. bradshawii* pollinators, flights that were coded as "A," indicating flights moving a greater distance away from the previous feeding stops. *E. decumbens* pollinators were also given differing values for A flights, due to the large difference in mean flight distances. Field crescents were given A values of 7.5 m, while all other pollinators were given A values of 1 m. (See the section called Erigeron Pollinators and Table 3.)

E. decumbens Seed Dispersal Measurement

The first attempt to measure *E. decumbens* seed dispersal was done using the same method that had been used with *L. bradshawii* seed. Seeds were dyed, and later the area around the plant was examined for the presence of dyed seeds. However, attempts to locate dispersed *E. decumbens* seeds were unsuccessful. (The *E. decumbens* seeds average 1.2 mm x 0.4 mm, while the *L. bradshawii* seeds average 10.1 mm x 5.6 mm.)

A second attempt was made to locate *E. decumbens* seeds by manually releasing dyed seeds and observing their movement in the field. First, the flower height of 106 *E. decumbens* flowers was measured to determine a mean flower height. Then, seeds were gathered from *E. decumbens* plants and placed in a plastic bag with a small amount of powdered dye. The bag was sealed and shaken to cause the dye to adhere to the seeds. A platform was established at the mean flower height. Wind speed was measured at this height, and the seeds were uncovered on the platform. With this method also, the seeds were too small to be observed. Also, there was concern that the seeds that traveled the shortest distance would be over-sampled using this method.

Finally, it was decided that the *E. decumbens* seed dispersal distance would be estimated using laboratory experimentation. *E. decumbens* seeds were gathered and stored in a sealed plastic container. Seeds that appeared to have their plumes intact were later selected from this set of seeds. A seed drop chamber was constructed from transparent plexiglass. The chamber's interior dimensions were 12.5 cm x 12.5 cm x 46.5 cm. The chamber was open at the top and the bottom. Black construction paper was placed on two sides of the chamber to aid in seed sighting. A paper platform was placed inside the chamber at a height of 25 cm. One at a time, seeds were placed on the platform then nudged off. The time for the seed to fall the 25 cm was measured to the nearest hundredth of a second. This measurement was combined with wind speed measurements to estimate *E. decumbens* seed terminal velocity, using a formula described below in the section *E. decumbens* Seed Dispersal Estimation..

Density Measurement

The density of *L. bradshawii* at Fisher Butte was measured directly. A 12 meter by 14 meter rectangle was established in a patch of *L. bradshawii,* where density was judged to be representative of within-patch density of the plant in this study area. Individual plants inside the squares were counted, and placed into three categories: vegetative only, flowering but producing little or no seed, and flowering and producing a strong seed crop.

Density of *E. decumbens* plants was estimated using the data of Ingersoll, et al. (1993). Because *E. decumbens* grows in clumps that may contain one or more individuals (Clark, *et al.*, 1993), it is difficult to estimate density. Ingersoll and her colleagues estimated the densities of several test plots at Fisher Butte and two other sites. The mean densities they found were 0.3 plants per m^2 at Fisher Butte, and 0.3 and 0.4 at the other two sites. A density value of 0.3 plants per m^2 was chosen as most representative of the patches of *E. decumbens* in this study and as a common density of *E. decumbens*.

E. decumbens Seed Dispersal Estimation

Plants have developed a variety of structures and mechanisms to enhance aerial seed dispersal. Species have been divided into groups based on the mechanisms their seeds use to disperse. These functional groups include dust seeds, plumed seeds, plane-winged seeds, and rotating-winged seeds. Small seeds known as dust seeds move based on viscosity of the air. Plumed seeds move based on their terminal velocity (Ward-Smith, 1984; Burrows, 1986).

Members of the Composite family have developed seeds that have plume structures attached to each seed. These plumes are called pappi (singular pappus). All Composites have a pappus, which is either scales or hair-like outgrowths that act either to protect the fruit or to aid in dispersal (Sheldon and Burrows, 1973). Of the species with pappi that aid dispersal, there are two functional groups based on the aerodynamic effect of the pappus. In one group, the pappus acts as a guide parachute. These species have small and comparatively porous pappi, whose effect is to orient the seeds. These seeds are dart-like, and generally do not disperse far from the parent plant. In the second group, the pappus acts as a drag parachute. The pappi of these species tend to be larger and more solid than those of the first group. Their function is to slow the fall of the seed so that horizontal wind motion can transport the seed a greater distance before it reaches the ground (Hoerner, 1958).

Burrows (1973) developed equations to model the behavior of plumed seeds. He proposed certain simplifying assumptions be made about the flight of a plumed seed. First, the effect of rotational motion by the seed may be assumed to be negligible. Second, it may be assumed that the horizontal movement of the seed is equal to the horizontal wind speed at all times after the seed is released. With these assumptions, he offered the following equation to calculate vertical motion:

$$Dv/dt = g - k(v + V_c)|v + Vc|,$$

where g is the acceleration due to gravity, v is the velocity of the seed in the vertical direction, V_c is convection velocity, and k is a constant based on the terminal velocity of fall for the seed, c, such that $k = g/c^2$. There are two components to the fall of the seed. First, the seed accelerates in a vertical direction until it reaches terminal velocity. This portion of the flight is termed transient motion. Second, the seed falls at terminal velocity, modified by convection, until it reaches the ground. Meanwhile, horizontal velocity is assumed to always be equal to wind speed.

Sheldon and Burrows (1973) measured the falls of 18 Composites. In the majority of the species they measured, "terminal velocity was reached so quickly that the distance-time curve as measured was indistinguishable from a straight line" (p. 669). This means that the seeds achieved terminal velocity so quickly that the amount of seed flight in which vertical acceleration took place is negligible. *E. decumbens* seeds were timed falling through a drop chamber as described in the section *E. decumbens* Seed Dispersal Measurement. These seeds fell with a mean terminal velocity of 0.42 m/s, similar to the terminal velocities measured by Sheldon and Burrows. It will therefore be assumed that transient motion is also negligible in the vertical movement of *E. decumbens* seeds. This further simplifies the predictive equations of Burrows (1973), to

$$v = c - V_c,$$

where c is terminal velocity, and V_c is convection velocity. Terminal velocity was measured for *E. decumbens* seeds as described above. Variation in convection velocity can have profound influences on the trajectories of plumed seeds (Burrows, 1986).

Horizontal wind velocity can be estimated from the records of a nearby weather station. The National Weather Service operates a weather measurement station at the Eugene Airport, approximately 8 kilometers north of the Fisher Butte site. Records were obtained from 1986 to 1995 for July and August. The records included the peak wind of each day. This measurement was taken at a height of 10 meters. Wind speed near the surface slows as elevation decreases, so a conversion factor must be used. For winds in the boundary layer, the lowest portion of the atmosphere, the logarithmic wind velocity profile function is:

$$u_z = u_*/k \ln(z/z_0)$$

where u_z is the mean wind speed at height z, u_* is the friction velocity, k is von Karman's constant (.42), and z_0 is the roughness length (Oke, 1990). The roughness length has been estimated for grasslands of .25 to 1.0 meter tall at 0.04 to 0.1 meters (Oke, 1990). The value of u_z can be estimated by inserting known wind velocity at a height z (Nieuwstadt, 1984). It will be assumed that below z_0, the seed is not moved horizontally by the wind. In order to predict wind speed at the height of release, wind velocities at the airport were used to develop a value for u_z, and that value was used to predict the mean wind speed at the height of seed release. Note that Oke (1990) further modifies the equation above by subtracting d, the zero plane displacement, from z, but this only applies to closely placed stands. The value of d is approximately two-thirds of the canopy height. However, the release height of *E. decumbens* seeds is less than d, and this would make wind speed negative. Wind was observed to be moving at the release height in direct correlation to winds above the canopy. The canopy at the Fisher Butte area is mostly composed of *Deschampsia cespitosa*, and is rather sparse near the *E. decumbens* plants. For these reasons, the equation does not include the term d.

Therefore, the final equations for this predictive model are:

$dy/dt = c$

$dz/dt = \int u_*/k \ln(z/z_0)$ from z = height of flower to $z = z_0$,

$dz/dt = 0$ from $z = z_0$ to $z = 0$.

The equation for neighborhood area requires the variance of seed distribution, so generating a mean seed dispersal distance will not be sufficient. The variance was estimated by selecting randomly variables of seed release height, peak wind speed, and seed terminal velocity. Seed release height and peak wind speed were used to predict the wind speed at the release height. Seed terminal velocity was used to determine the time required for the seed to reach the ground from the release height. This fall time was then placed into the equation for horizontal movement to predict the horizontal distance traveled in the fall time. This measurement was repeated 100 times, and this set of numbers is used to estimate actual seed dispersal variance.

Some critical assumptions underlie this method. As mentioned above, the equations for horizontal and vertical movement have been simplified using assumptions suggested by Burrows (1973) and Sheldon and Burrows (1973). The wind at the Eugene Airport is assumed to be an accurate approximation of the wind at the Fisher Butte site, and the wind speed at ten meters above a mowed lawn at the airport is considered similar to wind speed at ten meters above the prairie at Fisher Butte. Using the variance of these measurements to create an imaginary circle of neighborhood area ignores the directionality of the wind. The winds of July and August come most frequently from the north. (See Figure 5 for wind directions.) Thus, the seeds might be expected to disperse

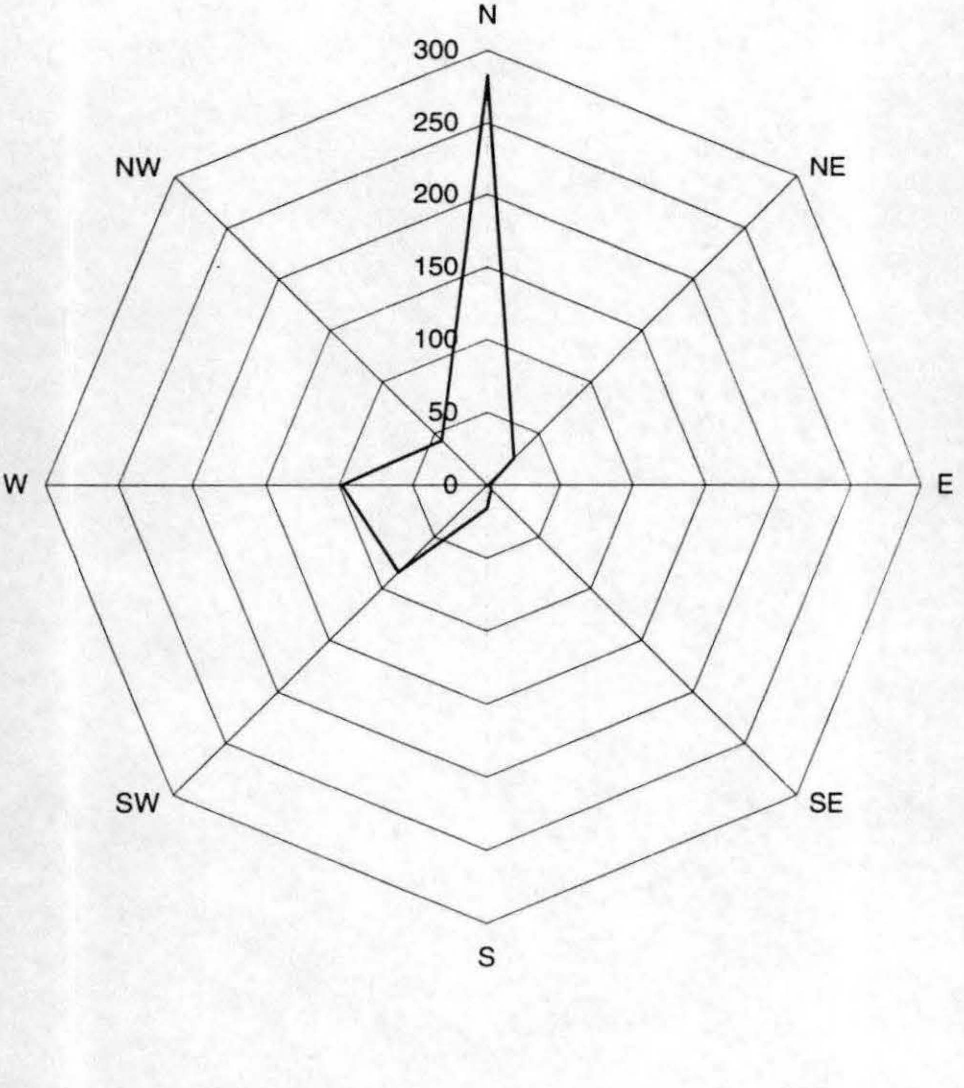

Figure 5. Direction of wind origin, July and August, 1987-1995, Eugene Airport National Weather Station.

generally toward the south, in more of an ellipse than a circle. This means that neighborhood area is slightly over-estimated. Finally, turbulence was not considered as a factor. Convection currents could lift *E. decumbens* seeds above their release heights, making dispersal distances much longer and impossible to predict (Burrows, 1986). It is likely that rare long-distance transport events are important parts of the ecology of *E. decumbens*, and most other plants, but such events are very difficult to predict, and should not be relied upon by resource managers (Howe and Smallwood, 1982).

CHAPTER VI

RESULTS AND DISCUSSION

Observation of pollinating insects led to new information about the frequency and behavior of insects visiting the study species. The data gained from pollinator observation were combined with estimates of seed dispersal to calculate neighborhood areas. Neighborhood areas were modified by correction factors created to estimate pollen carryover. These neighborhood areas under each carryover model were multiplied by density values to determine neighborhood sizes. The results of these calculations and their implications for *L. bradshawii* and *E. decumbens* are discussed below.

Insect Pollinators

L. bradshawii Pollinators

A total of 125 insects were observed visiting *L. bradshawii* flowers. Of these, 54 insects were tracked. Tracking involved following the insects at a discrete distance, and noting the stops they made on flowers or vegetation. The distances between stops was then measured and recorded, along with the species of flower visited, and whether subsequent stops were at the same flower, different flowers of the same individual plant, or flowers of different plants. Four genera of insects were judged to be important pollinators. Approximately 21 species were observed. See Table 1. (Some species were

TABLE 1. Insects observed on *L. bradshawii* flowers.

Insect Vistors	Percentage of all insects observed	Percentage of all insects tracked	Mean number of flights per sequence	Mean distance per flight (cm)	Percentage of stops at *L. bradshawii*
Heliophilus (*fasciatus* ?)[a]	20.49	44.44	5.83	75.05	69.28
Andrena [a] (2 spp.)	10.65	14.81	4.0	113.27	97.22
Small syrphid flies [a] (2 sp.)	5.73	11.11	3.67	67.65	56.00
Scatophaga (*stercoraria* ?)[a]	9.84	7.41	3.75	39.53	70.00
Other flies (6 spp.)	13.11	9.26	3.6	64.83	100
BEES					
Bombus sp.[a] (1 tracked)	1.64	1.85	3	92.67	75.00
Bombylius sp. (1 tracked)	0.82	1.85	2	46.50	100

TABLE 1. Insects observed on *L. bradshawii* flowers (continued).

Insect Vistors	Percentage of all insects observed	Percentage of all insects tracked	Mean number of flights per sequence	Mean distance per flight (cm)	Percentage of stops at *L. bradshawii*
Halictidae[a]	3.28	0			
Other bees (2 spp.)	4.09	7.41	8.0	29.22	83.78
Unknown wasp	0.82	0			
BEETLES					
Unknown beetle (green)	9.84	0			
Unknown beetle (copper) (1 tracked)	1.64	1.92	2	58.50	33.33
Unknown beetle (black)	18.03	0			

[a] These insects were observed with pollen on their bodies.

only observed on a few occasions, and specimens were not able to be taken, so identification is tentative.) The most common pollinator was a large syrphid fly of the genus Heliophilus. The species is probably *H. fasciatus*, or possibly *latifrons*. This species comprised 44.4% of the total tracked insects. Bees of the Andrena genus comprised 14.8% of the total tracked insects, with at least two species observed. Other, smaller syrphid flies were lumped into a single category, and comprised 11.1% of tracked insects. A Scatophaga species, probably *S. stercoraria*, a dung fly, comprised 7.4% of the tracked insects. No other insect was tracked more than twice. The four groups of pollinators together comprised 77.78% of the total tracked insects.

Heliophilus is probably the most effective mover of *L. bradshawii* pollen. It is approximately 8 mm long, around the size and shape of a house fly. The insect prefers *L. bradshawii* flowers to other species, visiting *L. bradshawii* on 69.28% of its stops. It was also observed stopping at a plant in the Cruciferae (mustard) family on 8.5 % of its stops. Another species of *Heliophilus*, *H. trivittatus*, is also known to feed on umbelliferous plants (the family of *L. bradshawii)* (Stanek, 1969), so it would not be surprising to find this species specializing on *L. bradshawii* flower feeding. The average distance moved by Heliophilus was 0.75 meters. Heliophilus tended to make more frequent stops on vegetation that most other pollinators, and these stops could have decreased their pollen load.

At least three species of the genus Andrena were observed. These are also likely to be effective pollinators. Andrena is a common genus, with over 550 species (Michner, *et al.*, 1994). Their mean distance traveled between stops was 1.13 meters. The bees spent less than 15 seconds at each stop, and frequently went beyond the nearest *L. bradshawii* flower for their next stop. They went around other flowers to reach *L. bradshawii* flowers. They visited *L. bradshawii* flowers on 97.22% of their stops.

Small syrphids were probably not very effective pollinators. They visited *L. bradshawii* flowers on 56.00% of their stops, and the mean distance between their stops was 0.68 meters.

The Scatophaga fly is an unexpected visitor on the *L. bradshawii* flowers. All adult Anthyomiids are carnivorous (McAlpine, 1987). It may be that this species is omnivorous, or that the species is attempting to capture other pollinators as they visit the *L. bradshawii*. They did tend to travel from one *L. bradshawii* flower to another, and did seem to be feeding on the flower. Pollen was observed on the insect.

E. decumbens Pollinators

A total of 177 insects were observed visiting *E. decumbens* flowers. The insects comprised approximately nine species. (Some species were only observed on a few occasions, and specimens could not be taken, so identification is tentative.) Of the species observed, a total of 113 were tracked. See Table 2. Tracking followed the procedures described above for *L. bradshawii* pollinators.

Three genera made up 89.09% of the insects tracked, and 90.40% of the species observed. The most common tracked and observed species was *Phyciodes campestris*, the field crescent, a native butterfly. The field crescent accounted for 40.91% of tracked insects, and 46.33% of observed insects. Second most common were Halictidae bees.

TABLE 2. Insects observed on *E. decumbens* flowers.

Insect Vistors	Percentage of all insects observed	Percentage of all insects tracked	Mean number of flights per sequence	Mean distance per flight (cm)	Percentage of stops at *E. decumbens*
Phyciodes campestris[a]	46.33	39.82	5.16	260.45	83.19
Toxomerus occidentalis[a]	12.43	10.62	11.67	20.32	92.31
Halictidae[a] (2 spp.)	31.64	36.28	4.27	19.56	97.01
Unknown syrphid fly	1.69	2.65	2.33	44.50	85.71
Unknown fly (gray)	1.13	1.77	4.0	13.43	100
Unknown fly (red posterior) (1 tracked)	0.56	0.88	3	109	100
Unknown bee-mimic fly[a]	3.39	5.45	3	22.81	88.24
Unknown fly (yellow)[a]	2.26	1.77	5	25.00	100
Unknown beetle (copper)	0.56	0			

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[a] These insects were observed with pollen on their bodies.

There were two sizes of Halictidae observed. The larger was around 7 mm long, and the smaller was around 4 mm long. It is not known if these are members of the same species, or of related species. Together, the small and large Halictidae were 37.27% of the tracked insects, and 31.64% of all observed insects. Third most common was a syrphid fly, *Toxomerous occidentalis*. It accounted for 10.91% of all tracked insects, and 12.43% of all observed insects. All other insects accounted for 10.91% of tracked insects, and 9.60% of observed insects.

Phyciodes campestris, the field crescent, is the most efficient transporters of *E. decumbens* pollen. This is a very common butterfly in the Pacific Northwest. The adult forms are seen from June through August, with latest observations occurring at higher elevation meadows. The larvae feed on *Aster conspicuus* and *Aster foliaceus*, and adults are known to favor Aster species and *Eriophyllum lanatum* (Christensen, 1981). Their movements between stops averaged 0.72 meters in length, longer than any other insect observed. *P. campestris* was observed in large numbers at the beginning of the field observations. In the final days of the field observations, none were observed. The butterflys' flights tended to be a series of 5 to 10 shorter flights, followed by a much longer flight that seemed to be scouting for other *E. decumbens* flowers. On several occasions, a *P. campestris* was observed to leave a flower and fly a loop of greater than ten meters, eventually returning to the exact flower from which they had started. The density of *P. campestris* was so high that they frequently encountered one another, and competition for flowers and possible mates frequently disrupted their flights. Pairs of *P. campestris*, presumably a male and a female, would often follow one another from flower to flower or plant to plant. When another male *P. campestris* approached a couple, the two males would generally fight until one retreated. *P. campestris* seemed to prefer *E. decumbens* to all other flowers in the prairie, although they generalized to other plant species more than any other major pollinator. Only 80.58% of their stops were at *E. decumbens* flowers. They also favored *Potentilla gracilis* flowers, making 12.07% of their stops there. When visiting either *E. decumbens* or *P. gracilis* flowers, the butterflies tended to stop at the same species on consecutive stops, rather than switching whenever convenient. They were observed to fly from one *E. decumbens* stop, around *P. gracilis* flowers, to another *E. decumbens* stop, and vice versa. The field crescents were most active when the weather was warmer and less cloudy, and took shelter on low vegetation in gusty winds. See Schmitt (1980) for a discussion of the impact butterfly behavior can have on neighborhood areas.

The Halictidae (sweat bees) were probably less effective at moving pollen, partially because of their smaller size compared to the field crescents, but also because they tended to make much shorter flights. The mean Halictidae flight was 0.13 meters. They were not observed making long foraging flights, although their smaller size did make such observations more difficult. The Halictidae tended to stay on a single flower for 15 to 30 seconds, then fly slowly to another flower, usually the nearest flower. They were not strong fliers. The Halictidae strongly preferred the *E. decumbens* flowers. *E. decumbens* were 97.01% of their stops. They were consistently observed throughout the flowering season. These insects were the only species observed on both *E. decumbens* and *L. bradshawii* flowers, and were observed only in small numbers on *L. bradshawii* flowers. Members of the Halictidae family generally nest in ground burrows. They may nest in such proximity that individuals share tubes that connect their burrows to the surface. The level of social interaction varies greatly between species. There are over 500 members of the Halictidae family in North America (Borror, *et al.*, 1989).

Toxomerous occidentalis, red syrphid flies, were observed later in the season. These insects are around 7 mm long, with spade-shaped, red-and-black striped thoraxes. They moved an average of 0.13 meters between stops, and stopped at *E. decumbens* flowers 92.31% of the time. They tended to move quickly between flowers, generally spending less than ten seconds between stops. This could mean that a *T. occidentalis* would move more pollen than a Halictidae bee in the same amount of time. They tended to visit flowers of one plant or patch rather thoroughly, often repeating visits to the same flowers, then move slowly and at low altitudes to another plant or patch. *T. occidentalis* was more easily startled than the ant-bees, and moved with great speed when startled. They were generally lost to the observer when disturbed, but probably moved two meters or more in an escape flight. This behavior would probably increase their actual mean flight distance from the observed data, but it is not known how often they would make escape flights in the absence of a human observer. *T. occidentalis* was observed feeding on old, withered flowers that no other pollinators visited.

Summary and Implications of Insect Pollinators

Both study species were visited by a variety of insects. *L. bradshawii* was visited by approximately 21 species and *E. decumbens* by approximately 10 species. Of these, 8 insect species were observed at *L. bradshawii* with pollen on their bodies, making them likely pollinators. At *E. decumbens*, 6 species were observed with pollen on their bodies. (See Tables 2 and 3.) Other species may also have been pollinators. For *L. bradshawii*, the species tentatively identified as *Heliophilus fasciatus* appeared to be the most effective pollinator. For *E. decumbens*, the butterfly *Phyciodes campestris* appeared to be the most effective pollinator, with the syrphid fly *Toxomerous occidentalis* also important.

The variety of insect visitors to both *L. bradshawii* and *E. decumbens* mean that both could be considered generalists in regard to their pollinators. However, the major pollinators of both species tended to favor the particular species, and were frequently observed traveling around flowers of other species to reach either the *L. bradshawii* or *E. decumbens* flowers. Therefore, the insects can be considered specialists in regard to the food sources they select.

The variety of insects observed, and the fact that many families of insects were observed, bodes well for the survival of these rare plants. Reliance on a single species, or on a set of species with similar life cycles and behaviors, would limit the ability of the plants to reproduce successfully in the event of reduction in the populations of such pollinators. For example, *Phyciodes campestris* was observed only on warm, sunny days. If *E. decumbens* depended on this one insect for pollination, an unusually cloudy or cold season might decrease the reproductive success of the plant. Fragmentation of habitat, introduced species, and human activity, such as agriculture, could easily cause local extinction of pollinating insects. In these cases, the presence of several species and a variety of families for both plants suggests that other insects would be able to pollinate *L. bradshawii* and *E. decumbens* in the absence of one or two of the species deemed important pollinators in this work.

Seed Movement

The seeds of *L. bradshawii* moved a mean distance of 22.46 cm. The movement was mostly to the south and southwest, although a significant number of seeds moved northeast of the parent plant. (See Figure 6.) The seeds spent a long time on the stalks after drying. Seeds began falling in June, and some seeds remained on the stalks when field observations ended in November. Generally, the paired seeds would split before falling, but around 5% of the pairs seemed to fall together. Several seeds were transported from the parent plant by the collapse of the stalk that still had seeds on it. These seeds were deposited close together around 25 cm from the parent plant.

The estimation of the *E. decumbens* seed movement resulted in a mean distance moved of 94.24 cm. These calculations did not include convection, nor the possibility of rare long-distance transport. Such movement is almost certain to occur in some circumstances, and may offer a possibility of genetic connection between patches that *L. bradshawii* does not have.

Density of Study Species

L. bradshawii density was measured in a representative part of a patch of the plant. Plants were recorded in three categories: vegetative only, flowering but producing

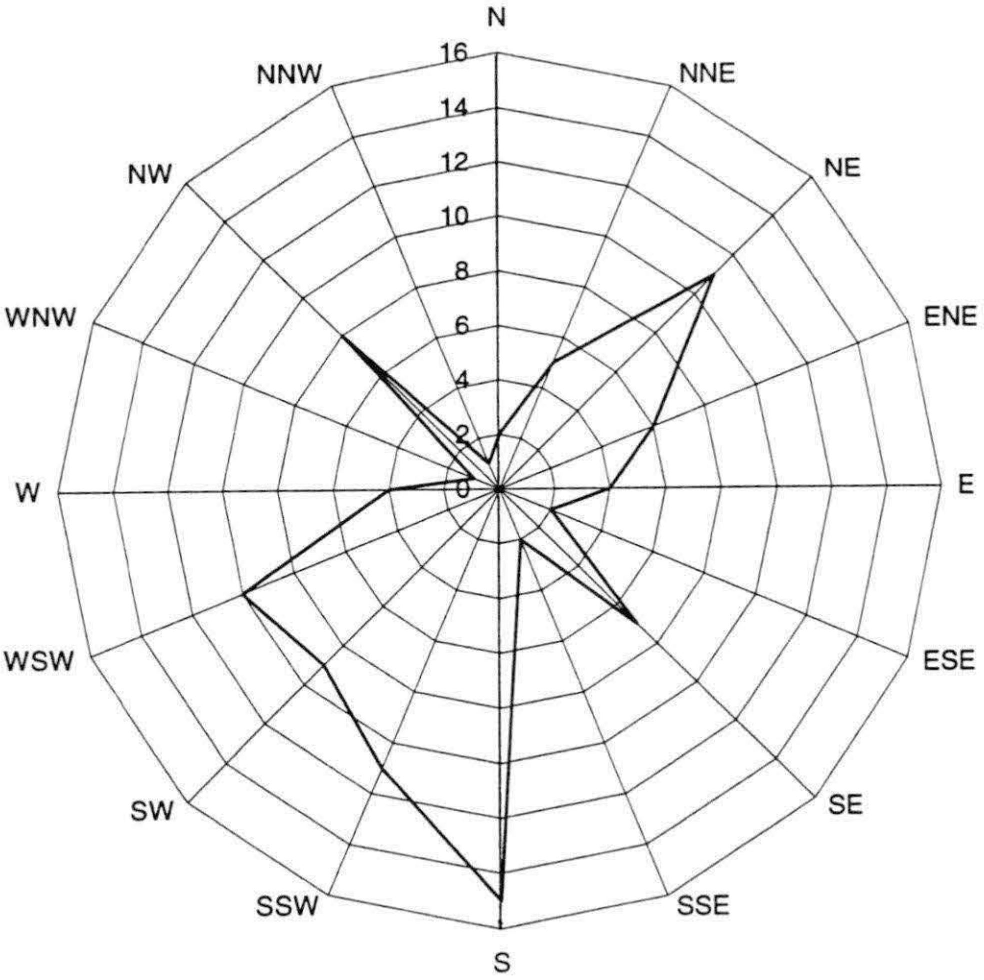

Figure 6. Direction of *L. bradshawii* seed movement.

little or no seed, and flowering and producing a strong seed crop. Within an area of 168 m^2 , there were 41 vegetative plants, 29 plants producing little or no seed, and 42 plants producing a strong seed crop. Thus, there were a total of 112 plants, and a total of 71 flowering individuals. The flowering individuals are the sexually mature individuals that are critical for determining neighborhood size, and their density is 0.42 plants per m^2. It was thought that weakly seeding plants might be more isolated than strongly seeding plants, but no pattern observed in the locations of either.

As explained above, *E. decumbens* density was estimated at 0.3 plants per m^2, based on the work of earlier researchers (Ingersoll, *et al.*, 1993).

Neighborhood Size and Area Calculations

Neighborhood areas have been calculated under three models of pollen carryover. (See Table 3.) These results can be compared to the neighborhood areas determined for other species. Knowledge of the neighborhood area and neighborhood radius of the plants may be helpful to resource managers in determining which patches might be expected to communicate genetic material. Also, the estimations of neighborhood area can be multiplied by the density of individuals to derive neighborhood size. This measure provides important clues to the viability of small isolated populations.

Note that for *E. decumbens*, the low-carryover condition has a smaller neighborhood area than the no-carryover condition. This is possible under the model because of stops at non-*E. decumbens* flowers and stops that return to the original flower of the sequence. For both of these conditions, the percentage of pollen that would have

TABLE 3. Neighborhood calculations for study species under three pollen carryover models.

	L. bradshawii	*E. decumbens*
Variance (pollen) (meters)	8.363	8.045
k (pollen)	2.085	2.858
Variance (seed)(m)	0.975	0.234
k (seed)	4	4
Density (plants per m^2)	0.42	0.3 [a]
Carryover Model Correction Factors		
NO	1	1
LOW	3.267	1.351
HIGH	7.846	2.375
Neighborhood Parameters Under Carryover Models		
NO		
Area (m^2)	39.646	36.118
Radius (m)	3.553	3.391
Size (in individuals)	16.651	10.835
LOW		
Area (m^2)	101.748	48.798
Radius (m)	5.691	3.941
Size (in individuals)	42.734	14.639
HIGH		
Area (m^2)	227.166	85.796
Radius (m)	8.504	5.226
Size (in individuals)	95.410	25.739

[a] Density was measured for *L. bradshawii*, and taken from Clark, *et al*., (1993) for *E. decumbens*.

been deposited at that flower is counted as zero. In the case of stops at non-*E. decumbens* flowers, the pollen is considered to be brushed off the insect's body just as it would be on an *E. decumbens* flower, but the pollen is lost to the *E. decumbens* population. In the case of flights that return to the original flower, the pollen is not lost, but the distance it is moved is zero. This model assumes that, in both cases, the pollen is lost permanently, not to be moved by subsequent pollinator activity. In the case of *E. decumbens*, the major pollinator, *I. icariodes fenderi*, had a comparably low percentage of stops on *E. decumbens* flowers (80%), which increased the frequency of pollen loss.

Smyth and Hamrick (1987) found neighborhood areas for *Carduus nutans*, musk thistle, to be between 67.7 m^2 and 251.8 m^2 based on pollen dispersal alone, and using different estimation procedures. Plumed seeds of this weedy plant disperse via wind to great distances, and seed dispersal alone produced a neighborhood area of 2189 m^2. Broyles and Wyatt (1991) found a neighborhood area for *Asclepias exaltata*, poke milkweed, of 23.3 m^2 when assuming no pollen carryover, and a neighborhood area of 159.6 m^2 when analyzing genetic similarity of offspring to estimate neighborhood size. Fenster (1991) examined the bee-pollinated *Chamaecrista fasciculata*, partridge pea, for four years. He found that pollen carryover increased the neighborhood area due to pollen by a factor of 3.4, and that the mean neighborhood area including seed dispersal was 17.6 m^2. Schmitt (1980) examined Senecio species, composites that are pollinated by both bees and butterflies, and found that neighborhood areas with only bees were between 0.69 and 7.3 m^2, while neighborhood areas with butterflies only were between 57.44 and 571.63 m^2 (not including seed dispersal). Other studies have also found neighborhood areas in the range of those reported here, and have found that increases in area due to pollen carryover are also in the range of those reported here (Campbell and Waser, 1989; Palmer, *et al.*, 1988; and Parra, *et al.*, 1993).

The radius of a neighborhood area can give an idea of the linear distance that genetic material may move. Due to rare long-distance transport, some pollen or seed may move beyond the radius of neighborhood area, but the amount of material that reaches beyond the neighborhood area is diminishing. Some material might be expected to move twice the radius of the neighborhood area, but it is doubtful that any material could move a distance ten times the radius (Lande, 1996, personal communication). Resource managers can use the values of neighborhood areas calculated here to evaluate the likelihood of communication between two patches of plants.

Neighborhood area multiplied by density of individual plants yields neighborhood size. Neighborhood sizes for *L. bradshawii* range from 17 to 95 individuals, while (see Table 3). Neighborhood sizes for *E. decumbens* range from 11 to 26 individuals. These values can be compared with work by Richards and Ibrahim (1978), who suggested that the mean neighborhood size for *Primula veris*, cowslip, was around 30, with values ranging from 5 to 200.

Implications of Neighborhood Calculations

The neighborhood areas calculated are comparable with the neighborhood areas that other researchers have found, as discussed above. However, the neighborhood sizes, derived by multiplying neighborhood area by density estimates, are more noteworthy.

The neighborhood sizes found for both *L. bradshawii* and *E. decumbens* are quite small, indicating that the plants are at risk due to inbreeding. As the pool of individuals with which to breed decreases, inbreeding increases. Inbreeding can be as extreme as selfing in plants, or can be matings with relatives. Inbreeding causes an increase in homozygosity. This decreases the variability between offspring. When offspring are more similar to each other, the chance that any of them can survive a change in their habitat is reduced (Williams, 1966).

Neighborhood size calculations can be used to estimate the potential for detrimental inbreeding. Neighborhood sizes reflect the number of individuals that might have an equal chance of parenting a given individual. The effective size of the population (N_e) is generally 0.1 to 0.8 times the size of the neighborhood (Crawford, 1984a). The results presented here suggest very small N_e values, which can mean that inbreeding may be a threat to the population. In order to avoid a decrease in adaptive potential as heterozygosity decreases, a minimum effective population size must be maintained. Some authors suggest that this minimum effective population should be around 500 individuals (Franklin, 1980; Soule, 1980), however, more recent work has suggested that a minimum of 5000 individuals is required to maintain genetic adaptability of the population (Lande, 1995). These results suggest that both of the study species have effective population sizes well under these suggested minima. Therefore, both species may be at risk for decreased adaptability through inbreeding.

A decrease in adaptability can be undetectable in a population until some habitat change has an unexpectedly severe impact. If inbreeding is more intense, inbreeding depression can occur. This is a "decrease in the mean value of a character," such as body mass or number of offspring produced, due to inbreeding (Lande, 1995, p.783). In populations that historically were outbreeding, a rapid change to inbreeding will cause the expression of recessive traits that may be detrimental or lethal. Also, mutations that are detrimental are maintained in small populations at a greater rate than in large populations. However, if populations increase their inbreeding gradually due to gradual reductions in population size, the lethal or nearly lethal recessive genes will be removed from the gene pool as the individuals that express the genes die before reproducing. Therefore, if inbreeding increases slowly, it is likely that the population will not have an abundance of lethal mutations (Lande, 1995). In the case of gradual increases in inbreeding, it is likely that mildly detrimental genes will be expressed more frequently, and loss of variability will further reduce the ability of a population to survive environmental changes or climatic variability.

Both study species are likely to have experienced both gradual declines in population due to competition from invasive species and sudden declines in population due to habitat loss and fragmentation. Populations that are known to have decreased in size suddenly might be expected to experience greater inbreeding depression than those that decreased gradually. All populations of both species are likely to be at a high risk for inbreeding depression. As explained above, the effects of this may not be visible until some environmental change has a severe effect on individuals. Resource managers should be aware of a potential lack of resiliency to change in both species.

IUCN Red List Categorization

Both study species can be evaluated using criteria developed by the International Union for the Conservation of Nature (IUCN) to measure the level of extinction threat a species faces. The IUCN has developed a set of categories that characterize the extent of threat to any species. These categories are internationally recognized and provide a valuable standard for measurement of extinction threat. According to the revised criteria (IUCN, 1994, pp.15-21), both *L. bradshawii* and *E. decumbens* can be considered Critically Endangered, based on the same criteria. *L. bradshawii* has an area of occupancy of 1.34 km^2 (331 acres), an estimated 52,250 individuals, and 14 populations (Parenti, *et al.*, 1993). *E. decumbens* has an area of occupancy of 1.36 km^2 (335 acres), an estimated 7518 flowering clumps, and 18 known populations (Clark, *et al.*, 1993). Both have an area of occupancy of less than 10 km^2, the known populations are severely fragmented, and there is a continuing decline in suitable habitat, by reduction in extent and quality. Also, the number of individuals in some sub-populations is so small that a continuing decline in the number of sub-populations can be projected. (For both species, botanical research in recent years has discovered new sub-populations, but this discovery period seems to have ended, and the discovery of previously unknown sub-populations does not imply that the number of sub-populations is increasing or remaining constant.) Placement in the category Critically Endangered means that a species faces "an extremely high risk of extinction in the wild in the immediate future" (IUCN, 1994, p. 15).

CHAPTER VII

SUMMARY

L. bradshawii and *E. decumbens* are two rare plants of the wet prairie of the Willamette Valley, Oregon. Their habitat has decreased greatly in size over the past 200 years, due to human activities in the valley. As a result, both plants exist in scattered patches. In these circumstances, reproduction may be impaired, either by a loss of pollinating insects, or by a gradual loss of adaptability due to inbreeding.

The reproductive aspects of these two study species were examined. Pollinating insects were observed and tracked in the field. Both plants were found to have several pollinating insects. Insects were generally observed to specialize on one of the study plants. Seed dispersal was measured in the field for *L. bradshawii* and estimated for *E. decumbens*.

The measurements of pollen dispersal and seed dispersal were used to calculate neighborhood areas. This is a measure of the area of a circle from which the parents of an individual at the center of the circle could be randomly selected. A range of neighborhood area was calculated for both species, depending on the assumed amount of pollen carryover that might occur as insects moved from flower to flower. The measurements of neighborhood area were comparable with neighborhood area measurements done by several other researchers.

Density of *L. bradshawii* was measured in the field. Density of *E. decumbens* was taken from the work of other researchers. Neighborhood area multiplied by density yields neighborhood size. This is the count of individuals in the neighborhood area. Neighborhood size was small for both species, indicating that inbreeding depression is quite possible for both species. Inbreeding depression results in a lack of adaptability that often is first evidenced with unexpectedly severe population decreases in the wake of some environmental change.

The results presented here should only be considered as a general approximation of actual reproductive abilities of the study species. Reproduction of these plants involves a large number of variables that could alter the distances pollen and seeds move. Weather variability can impact reproduction in a variety of ways. Weather patterns influence the duration of flowering, the timing of flowering (which can determine which insects are available to pollinate), insect behavior (because windy conditions can prevent some insects from flying), and the distance and direction of wind-dispersed seed travel. Different sites (or the same sites in different years) may have different insect communities, and those insects may have different abilities to move pollen. Also, density of the plant species may well impact the behavior of the insects (Beattie, 1976). Finally, environmental changes may impact insect behavior. For example, insects might be less likely to cross a stream or a road than to travel a similar distance across the prairie. All these factors make the results from a one-season, one-site study less reliable. However, it is hoped that these results offer general guidelines of what to expect in reproduction of these two rare species.

APPENDIX

CORRECTION FOR KURTOSIS

Kurtosis Calculations

Both pollen and seed dispersals have been shown to have non-normal distributions (Levin and Kerster, 1974). Typically, these dispersals are leptokurtic. In order to control for leptokurtosis, a correction factor, *k*, is added to the formula for neighborhood area. Wright (1969, corrected 1977) developed a method for calculating *k* which involves several steps.

A distribution can be expressed by the formula:

$$y = y_0 \exp(-bx^{1/a}).$$

In the case of a normal distribution, $a = 0.5$. If $a > 0.5$, the distribution is leptokurtic, and if $a < 0.5$, the distribution is platykurtic. In order to estimate *k*, the value for *a* must first be found, and in order to find *a*, the value for *gamma* must first be found.

Leptokurtosis is represented by γ_2

$$\gamma_2 = [n\Sigma x^4/(\Sigma x^2)^2] - 3.$$

(This assumes that movement is in random directions.) For a normal distribution, $\gamma_2 = 0$. The value of γ_2 can be used to estimate the parameter *a* from the first equation. The following formulae estimate *a* with a 1% error:

$$\log_{10} a = .0341 \log_{10}(\gamma_2) - 0.156, \quad \text{for } 1 < \gamma_2 < 15,$$

$$\log_{10} a = .0295 \log_{10}(\gamma_2) - 0.097, \quad \text{for } 15 < \gamma_2 < 50.$$

Then, the value for *a* obtained by the process above is used to calculate a leptokurtic neighborhood area:

$$A_l = 2^{2a}[\ \Gamma(2a+1)\,\Gamma(a) /\ \Gamma(3a)]\ \pi\ \sigma^2$$

For all calculations, numbers were rounded off to the nearest thousandth, and gamma functions were evaluated using tabulated values in Davis (1965). If the distribution is normal, and $a = 0.5$, this reduces to $A = 4\ \pi\ \sigma^2$, the neighborhood area for a normal distribution.

Finally, the correction factor, *k*, is defined as

$$k = 4\ (A_l / A),$$

where $A=4\ \pi\ \sigma^2$.

The numeral four is in the equation because Crawford (1984a) simplifies the equation by removing that numeral while adding the correction factor, so that $A=4\ \pi\ \sigma^2$ becomes $A=k\ \pi\ \sigma^2$. Thus, k=4 in a normal distribution.

Calculating Kurtosis Correction Factors

L. bradshawii Kurtosis

For *L. bradshawii* seed kurtosis, the distances of seed dispersal were used to calculate γ_2 . This value was -1.277, and so was not leptokurtic. Therefore, the correction factor *k*(seed) is equal to 4 (See Table 4.)

Table 4. Kurtosis calculations.

	γ_2	a	k
Lomatium			
Pollen	150.2886	3.2510	2.08
Seed	-1.277	not leptokurtic	4
Erigeron			
Pollen	39.1031	2.3589	2.858
Seed	-0.9482	not leptokurtic	4

For *L. bradshawii* pollen kurtosis, calculation of *k* was more complicated. Only the flight distances of those flights that involved five or more stops at flowers were used to estimate pollen carryover were used to estimate kurtosis. Overall kurtosis was calculated for high, low, and no carryover models. The k-values for are shown in Table 4. In addition, kurtosis of individual insect flights was measured. Correction factors were calculated for each major pollinating insect, and for high, low, and no carryover models. For each model, only the distances used to calculate carryover were used to calculate kurtosis. Most distributions of individual insect distances were close to normal.

In the high pollen carryover model, the Heliophilus species had a k value of 3.042, and in the low carryover condition, the Andrena had a k value of 3.773. No other k values were more than 3% different from k = 4, a normal distribution.

$$A = k \pi \sigma^2$$

Of the 79 flights used to model carryover, the proportion of flights by each pollinator was determined. This proportion, multiplied by the neighborhood area for each insect, yields the proportion of the total neighborhood area due to pollen and due to the specific pollinator. The sum of all those proportions yields the total neighborhood area. Note that this assumes that the proportion of each insect comprising the flights used to model carryover is the same as the actual proportion of each insect's role in moving pollen. It is doubtful that this is accurate, and hypothetical cases were also modeled, giving values for neighborhood areas with estimated values for the proportion of pollen moved by each insect.

E. decumbens Kurtosis

E. decumbens seed distribution was normal, so k(seed) was set at 4.

E. decumbens pollen distribution was predicted in the same manner as was *L. bradshawii* pollen distribution. Overall k values were obtained for high, low and no carryover models. Values for k were also calculated for each pollinating insect.

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