LIFE HISTORY AND MODELING OF AN ENDANGERED PLANT, *PENSTEMON HAYDENII*

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LIFE HISTORY AND MODELING OF AN ENDANGERED PLANT,

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The demography of the federally listed endangered species blowout penstemon (*Penstemon haydenii* S. Watson) was quantified from 2005 through 2007 by the survival and growth of marked plants in the Nebraska Sandhills. Factors hypothesized to affect plant fecundity, seed viability, and seed germination rate were tested experimentally for their effect on population growth rate (λ). Average seed production was 518 (SE = 29.01) seeds per stalk across all blowouts for 2005, 2006, and 2007. Experimental treatment with fungicide, insecticide, or both did not reduce damage. Therefore, no differences emerged in seed output, weight, or viability. However, herbivore, granivore, and fungal impacts were significant in some sites. These interactions may be important to population persistence if surrounding vegetation invades blowout penstemon habitat, and increases herbivore habitat. From 14 to 81% of seed buried in permeable enclosures were found to remain viable for 2.5 years, suggesting that a seed bank is possible. However, most field-planted viable seed germinated within the first year and post-dispersal seed losses did occur, which resulted in minimal seed remaining in the soil. Simulated grazing experiments produced no significant differences between clipped or control treatments in mean plant survival, flowering stems, flowering stem height, or number of verticillasters after either the first or second growing season. Spring clipping

of flowering blowout penstemon plants was not detrimental to plant survival or reproductive capacity in the subsequent year. Using a Lefkovitch stage based matrix model, the population growth rate of blowout penstemon averaged over all test populations was found to be negative from 2005 to 2006 and positive from 2006 to 2007. Tests varying matrix parameters across a range of values indicated that the juvenile stage is important for long-term survival. The initial population size made little difference in the survival potential of populations in individual habitat fragments. Adjusting carrying capacity to simulate loss of habitat suggested that a closer look at habitat persistence is important to predicting demographic outcome for blowout penstemon.

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DEDICATION

To my husband, Joe and to my children Jim, Dan and Mandy for their love support and patience.

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Chapter 1: Introduction and Outline

The Species

Claude Barr (1983) described blowout penstemon (*Penstemon haydenii* S. Watson) as the "most distinctive, intriguing and beautiful of penstemon species" and "delightfully fragrant." One of 275 species in the genus *Penstemon* endemic to North America, blowout penstemon and only one other species are fragrant. Historical data suggest the genus *Penstemon* spread east from the Rocky Mountain/Columbia Plateau region (Pennell 1935, Wolfe et al. 2002). Blowout penstemon, is endemic to the Sandhills region of Nebraska and to sand dunes in Carbon County, Wyoming.

The genus *Penstemon* has been traditionally placed in the family Scrophulariaceae, for which recent genetic tests have discovered several distinct monophyletic groups (Olmstead et al. 2001). Judd, et al. (1999) have placed *Penstemon* in the family Plantaginaceae. Alternative placements have been suggested (Olmstead et al. 2001). The lineage of *Penstemon haydenii* from Order: Lamiales, Family: Schrophulariaceae, Tribe: Cheloneae, Genus: *Penstemon*, Subgenus: Penstemon, Section: Coerulei, Species: *Penstemon haydenii*.

Blowout penstemon was possibly first collected in 1857 by Ferdinand V. Hayden (Sutherland 1988) and incorrectly ascribed the name of *Penstemon acuminatus*. It was later given the name of its collector, Hayden, when a new specimen collected by Herbert J. Webber in Thomas County, Nebraska in 1891 revealed blowout penstemon as a unique species (Sutherland 1988). The Webber specimen was more complete than the Hayden specimen and was described to include flowers, fruits, and rhizomes (Sutherland 1988).

Current morphological descriptions report a deep taproot and stems which root adventitiously in shifting sand (Great Plains Flora Association 1986).

Blowout penstemon is a perennial species with firm, glabrous, and somewhat glaucous leaves and stems which become decumbent at the base. This semi-evergreen plant produces new shoots from buds formed at the base of stems the previous year (Lamphere 1999, Stubbendieck and Kottas 2007). Seeds typically germinate in the spring, and plants remain vegetative in the first year. These plants typically flower in the second or third year (Flessner 1988). Initiation of flowering induces the leafy bracts of vegetative shoots to broaden and become taller, producing an indeterminate thyrse inflorescence with verticillasters (Great Plains Flora Association 1986). A verticillaster is a pair of cymes subtended by leaves or bracts which form a false whorl (Baranov 1969). Each cyme holds 4 to 6 fragrant blue, lavender or pink bilabiate flowers (Kaul et al. 2006). Capsules have two chambers and are septicidal. Flowering shoots producing capsules often remain erect until the following summer or longer.

HABITAT

Blowout penstemon grows in the Sandhills region of north-central Nebraska and the northeastern Great Divide Basin in Carbon County, Wyoming. This research was conducted in Nebraska Sandhills, an area of stabilized sand dunes covering 5 million ha (Swinehart 1990). It is the largest area of sand dunes in the Western Hemisphere (Kaul et al. 2006). The Ogallala Aquifer lies below these dunes and provides many ponds, fens, and other shallow freshwater features which support plant life. The Sandhills prairie is Nebraska's "best preserved prairie ecosystem" (Kaul et al. 2006). Sandhills vegetation is

a mixture of mid-sized and tall grasses, with about 600 native species, which is fewer than in the tallgrass prairie to the east (Kaul et al. 2006).

Vegetation in the Sandhills is dominated by a matrix of mixed grass prairie. Pool (1914) described the Sandhills prairie as a bunchgrass association dominated by tall grasses such as sand bluestem [*Andropogon gerardii* subsp. *hallii* (Hack.) J. Wipff], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], swtichgrass (*Panicum virgatum* L.), and indiangrass [*Sorgahstrum nutans* (L.) Nash], and mid- and short grass species such as little bluestem [*Schizachyrium scoparium* (Michx.) Nash], sand lovegrass [*Eragrostis trichodes* (Nutt.) A. W. Wood], needle-and thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], and blue grama [*Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths].

The common name of blowout penstemon comes from the blowouts of the Sandhills. Pool (1914) described it as one of the “more common and typical species” in blowouts. Blowouts are areas of round or conical depressions formed in the sand when prevailing northwesterly winds scoop out the sides of the hills (Pool 1914). These eroded areas form on the sides of dunes when vegetative cover is removed or disturbed and wind action further exposes the slopes (Stubbendieck et al. 1989). Blowout penstemon is a pioneer species in these blowouts, often found among blowout grass [*Redfieldia flexuosa* (Thurb.) Vasey], another pioneer species and often the first pioneer in a blowout (Pool 1912). Sandhill muhly (*Muhlenbergia pungens* Thurb. *ex* A. Gray) is a successor to blowout grass with more compact growth and a more efficient root system (Tolstead 1942). Neither blowout grass nor blowout penstemon persists in the sand muhly stage of succession (Pool 1912, Tolstead 1942).

Fire and heavy concentrations of grazing animals were two causes of disturbance (Pool 1914). At the beginning of the 20th century, a grazing economy began to replace traditional agriculture (Tolstead 1942). Reduced fire frequency and current range management practices have increased vegetative cover, reduced blowout formation, and, thus, the habitat for the blowout penstemon (Sylvester 1957, Weedon et al. 1982). Human efforts to reduce fire (Bragg 1985) have reduced bare, blowing sand, confining blowout penstemon to isolated patches with little chance of migrating to new habitat (Stubbendieck and Kottas 2007).

LIFE HISTORY AND MODELING

The Endangered Species Act (ESA) exists "to provide a program for the conservation of such endangered species [U.S. Fish & Wildlife Service (USFWS) 1985]." When a plant is listed as endangered, Section 4(f) of the Endangered Species Act directs that a recovery plan be developed to promote conservation of the species. Included in this recovery plan are measurable criteria which, when met, would result in a determination that the species be removed from the list (USFWS 1985). Blowout penstemon was listed as a Federally endangered plants species in 1987 under the protection of the Endangered Species Act of 1973 (USFWS 1987). A recovery plan was approved on July 17, 1992 which sets the criteria that must be met for consideration to reclassify and delist blowout penstemon. The objectives of the recovery plan were reclassification from endangered to threatened with a minimum of 10,000 individuals in at least five stable populations and delisting with 15,000 individuals in ten population groups. The projected period required for each of these objectives was 10 and 15 years

respectively. Specific criteria which must be met for delisting are as follows (Fritz et al. 1992):

- "A total population of at least 15,000 established individuals with documented stability.
- A minimum of 10 population groups, each with a minimum of 300 plants at low point of population fluctuations, that are documented to be naturally-reproducing and self-sustaining. These groups will be comprised of naturally occurring, extant population groups, population groups reintroduced into area of historic occurrences, and population groups introduced to new locations within the species historic range in order to ensure demographic stability. In total, these groups should represent a viable population that is demographically stable, able to maintain genetic variation, and evolve. They should be able to withstand and adapt to significant natural disturbances and environmental variations.
- A minimum level of protection that will ensure the continued viability of each population group. The highest level of protection should be afforded the above 10 population groups to prevent their destruction, habitat degradation or exploitation, and guarantee their status as a viable population.
- A management plan is established and implemented for each population group that will maintain it as a naturally reproducing, self-sustaining population. The plan should enable the group to evolve and withstand natural disturbances and environmental variations in its habitat."

An outline of recovery actions lists seven steps (Fritz et al. 1992), all of which have received some research attention:

1) Protect current populations
2) Locate additional existing populations
3) Monitor populations and conduct research to determine species life history
4) Reintroduce populations and introduce new populations
5) Develop management plans
6) Maintain seed source
7) Carry out public education in support of conservation.

Species life history, within action 3, has received little attention. Other necessary recovery actions are studies to determine the effects of grazing, germination and establishment under natural conditions, seed banking and viability, insect pests, and diseases.

Plant life history is the basis for which plant sustainability can be assessed. All plant populations face some risk of decline or extinction from natural processes, even without human intervention (Burgman et al. 2001). Conservation goals should not only diagnose and halt the cause of population decline, but also account for demographic and environmental stochastic events which lead to decline or extinction (Caughley 1994). These environmental and demographic variations can be approximated by population models (Burgman et al. 2001). Models simplify the real world and reveal assumptions of how the investigator conceptualizes a process (Mohler 1993).

Understanding the life history of endangered species is central to understanding the causes responsible for its decline. The first step is conducting a survey and

monitoring populations, but efforts must go beyond that, not only increasing plant numbers, but also understanding the processes that govern their existence with or without human intervention. The status of population fluctuations and current growth trends may be the most biologically relevant question when evaluating rare plants (Schemske et al. 1994). Demographic parameters drive the growth rates which are crucial to understanding population persistence (Goodman 1987). Freville et al. (2007) found that extinction risk typically involved interaction of at least one extrinsic (environmental) threat variable and one intrinsic life history trait. There is a need to understand whether the effect of the organism itself or environmental variation determines population fluctuations (Thomas 1990). While genetic isolation is one concern for this species (Stubbendieck et al. 1997a), the persistence of geographically isolated species is likely to depend more upon demographic traits and population dynamics than genetics (Lande 1988). Caughley (1994) outlined four steps to identifying agents of decline: 1) understand the ecological context and status of a species by studying its natural history, 2) list conceivable agents of decline, 3) measure past and current status levels to identify agents of decline, 4) experimentally test hypotheses to confirm agents of decline. Caughley (1994) emphasized that the most important steps were 1 and 4, for without adequate life history data, the wrong hypotheses may be selected. In 2006, the total number of blowout penstemon plants was 20,567 (Stubbendieck et al. 2007). If for instance, that population size alone is equated with recovery, without understanding the life history and agents of decline, there is a risk of repeating mistakes made in the case of the California condor (*Gymnogyps californianus* Shaw) where assumptions made about

the causal agent of decline prevented the timely scientific discovery of the true agent of decline (Caughley 1994).

Crawley (1990) emphasized the need to develop theoretical models specifically for plants, based on key aspects of their biological traits that make them, as sessile organisms, fundamentally different from animals. For instance, knowledge of seed fate is essential to conservation efforts (Chambers and MacMahon 1994). The importance of size to fecundity (Lacey 1986, Clauss and Aarssen 1994) and to competition and density (Weiner 1993, Damgaard et al. 2002) make it an important measure of life history.

The overall goal of this dissertation is to assess the life history and viability of current blowout penstemon populations. The outcome will be greater understanding of blowout penstemon life stages, suggestions for future life-stage conservation goals, new data to address target population numbers, and assessment of the current recovery goal of 300 as a low point for each of the ten population groups (Fritz et al. 1992). Viability is explored using a stage model approach to assess the life stages of this plant. The stage based approach to modeling life stages requires the measurement of plant densities and quantitative estimates of the number of viable seeds, total seeds per plant, and seedling establishment rate per viable seed (Menges 1990). Several populations were followed to determine life stages, examine the potential for a seed bank, and assess germination and survival rates of the various stages. The influence of granivory, herbivory, fungal disease, and grazing on fitness is explored. This modeling effort will assist future conservation strategy and provide another example for assessing other endangered or threatened species.

Productivity of blowout penstemon is quantified in Chapter 2 and measures of fecundity are given. Population monitoring since the early 1990s has followed the numbers of vegetative and flowering adults and can be used to analyze potential seed production, but has not included data that follows individuals through life stages. The recovery plan estimates capsules contain from 25 to 35 seeds (Fritz et al. 1992). Fritz et al. (1992) attributes a mean count of 1500 seeds per plant to Flessner (1988). However, Flessner found only 576 seeds per plant. The count of 1500 seeds may have come from an unpublished count by Ronald Weedon (J. Stubbendieck, *personal communication*). Seed counts were conducted to determine a more accurate representation of that approximation. Further explained in Chapter 2 are insect herbivory and fungal activity on seed production and viability. Herbivory and granivory may affect the potential for a seed bank, the potential for germination, and ultimately the potential for survival of rare species. Insect and fungal exclusion studies were conducted to examine their effects on floral stalk heights and numbers of verticillasters, capsules, and seed. Viability studies were conducted to help determine seed bank and germination potential, which was the focus of Chapter 3.

Short-lived perennial plants are often scattered into fragmented habitats and rely on seed for reproduction (Louda and Potvin 1995). Researchers to date have suggested that while this plant produces seeds which may survive for many years (Stubbendieck et al. 1997b), a significant seed reserve has not been found (Flessner and Stubbendieck 1988), and vegetative reproduction is more likely than reproduction from seed (Stubbendieck et al. 1983, Stubbendieck and Weedon 1984). Naturally occurring seedlings were reported to be rare due to lack of moisture, and dormancy factors

(Stubbendieck at al. 1983, Stubbendieck and Weedon 1984, Lamphere 1999). In direct seeding experiments only 5 of 20,000 seeds produced seedlings (Stubbendieck et al. 1993). To test these hypotheses, a seed burial experiment (Section 1 of Chapter 3) was conducted to determine whether buried remains viable long enough to produce a seed bank. Tetrazolium testing was used to assess viability. The hypothesis that field germination is rare (Stubbendieck et al. 1983) is examined in Section 2. Also, germination and seedling survival rates are quantified, under field conditions, both with and without predation, to determine likelihood of seed available for banking. In experiments designed to keep seeds free from predators and from blowing away, the number of seeds likely to germinate or remain in the seed bank from any one cohort was determined. Allowing predation in these same experiments, also produced data to assess the effect of predation on the seed bank and on seedling establishment.

The impact of grazing on fecundity is investigated in Chapter 4. Ranching is the primary economic resource of the Sandhills region (Fritz 1998, Wishart 2004). Therefore, it is necessary to determine if management for this species can be coordinated in a positive way with management for ranching. The impact of grazing on this plant species and its habitat will be a key factor in effectively managing its populations. Clipped and unclipped plants of similar size were paired and compared for recovery potential of adult plants and for their ability to produce new flowering shoots in subsequent years.

The parameters necessary to build a life stages model for blowout penstemon are quantified in Chapter 5. It describes the test of a hypothesis designed to determine which stages exist and the probability of survival to the next stage. A mapping and tagging