Aquilegia chrysantha A. Gray var. *rydbergii* Munz (Rydberg's golden columbine): A Technical Conservation Assessment

Prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project

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AUTHOR'S BIOGRAPHY

Juanita A. R. Ladyman received her B.Sc. degree (with First-class honors) in Biochemistry from London University, England. Her first professional position was as plant pathology laboratory technician and, later, as greenhouse research supervisor with the Arid Lands Research Center on Sadiyat Island in the United Arab Emirates. She obtained her Ph.D. degree in Botany and Plant Pathology from Michigan State University where she was also a research assistant with the D.O.E. Plant Research Laboratory. She worked as a plant physiological ecologist and plant scientist for Shell Development Company conducting research on the physiology, ecology, and reproductive biology of economically important plant species and their wild relatives. She then worked for a plant biotechnology company in their Genetic Transformation and Plant Tissue Culture Division. For the last 13 years she has worked in the area of conservation, particularly on rare, endemic, and sensitive plant species in the southwest United States. For three years of that time, she was the botanist with the New Mexico Natural Heritage Program. She has conducted research and monitoring programs on both non-vascular and vascular species. She currently is a partner in *JnJ Associates* LLC, an environmental consulting company in Colorado.

COVER PHOTO CREDIT

Aquilegia chrysantha var. *rydbergii* (Rydberg's golden columbine). Photograph by the author.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *AQUILEGIA CHRYSANTHA* VAR. *RYDBERGII*

Status

Aquilegia chrysantha var. *rydbergii* is endemic to central Colorado. The NatureServe Global rank for this variety of an otherwise apparently secure species is critically imperiled (G4T1Q). The letter "Q" is used after the rank value because the distinctiveness of the taxon at the current level is uncertain. *Aquilegia chrysantha* var. *rydbergii* is ranked critically imperiled (S1) by the Colorado Natural Heritage Program. The USDA FS Region 2 Regional Forester (USDA Forest Service 2003a) and the USDI Bureau of Land Management Colorado State Director (USDI Bureau of Land Management 2000) designate it a sensitive species.

Primary Threats

Aquilegia chrysantha var. *rydbergii* is most vulnerable to habitat loss caused by activities associated with recreation. Much of the habitat for this taxon has already been severely altered and degraded. Occupied habitat on the Pike-San Isabel National Forest is currently managed primarily for recreation. Hiking, biking, and horse-riding trails go through the existing occurrences. Habitat encroachment by invasive weeds and livestock grazing are other potential threats. Long-term population sustainability may be vulnerable to declines in pollinator populations. As urbanization encroaches upon natural habitat, introduction of horticultural varieties of *A. chrysantha* may also become a concern. These varieties could hybridize with the natural populations and thus cause genetic dilution.

Primary Conservation Elements, Management Implications and Considerations

The uniqueness of the taxon, *Aquilegia chrysantha* var. *rydbergii*, is disputed. Many botanists consider that the differences observed (principally smaller flower size, blunter sepals, highly curved dried fruits, and smaller, bluish leaf segments) fall within the normal range of variation for the species *A. chrysantha*. However, these Colorado populations are notable in that they are disjunct, isolated, and at the northern edge of the eastern range of *A. chrysantha*. A conclusion from demographic research, which has significant conservation implications for all isolated populations of *A. chrysantha*, is that re-colonization of sites from which populations are extirpated will not occur naturally. Extirpation of isolated populations is likely to lead to a significant loss of genetic diversity.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). *Aquilegia chrysantha* var. *rydbergii* (Rydberg's golden columbine or golden columbine) is the focus of an assessment because it is a rare taxon endemic to west-central Colorado (Spackman et al. 1997) and because it is designated sensitive in USFS Region 2. A sensitive species is a plant or and animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution (FSM 2670.5 (19)). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations. Rather it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e. management implications). Furthermore, it cites management recommendations proposed elsewhere and examines the success of those recommendations that have been implemented.

Scope

This assessment examines the biology, ecology, conservation status, and management of *Aquilegia chrysantha* var. *rydbergii* with specific reference to the geographic and ecological characteristics of the USFS Region 2. Although some of the literature relevant to this taxon may originate from field investigations outside the region, this document places that literature in the ecological and social context of the central Rocky Mountains. Similarly, this assessment is concerned with the reproductive behavior, population dynamics, and other characteristics of *A. chrysantha* var. *rydbergii* in the context of the current environment rather than under historical conditions. The evolutionary environment of the taxon is considered in conducting this synthesis, but it is placed in a current context.

In producing this assessment, I reviewed peer-reviewed (refereed) literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on *Aquilegia chrysantha* var. *rydbergii* may be referenced in the assessment, but an effort was made to consider all relevant documents. The assessment emphasizes the peer-reviewed literature because this is the accepted standard in science. Some non-refereed literature was used in the assessment because information was unavailable elsewhere. In some cases, non-refereed publications and reports may be regarded with greater skepticism. However, many of these are often 'works-in-progress' or isolated observations on phenology or reproductive biology and are reliable sources of information. For example, demographic data may have been obtained during only one year when monitoring plots were first established. Insufficient funding or manpower may have prevented work in subsequent years. One year of data is generally considered inadequate for publication in a peer-reviewed journal but still provides a valuable contribution to the knowledge base of a rare plant species. Unpublished data (for example, Colorado Natural Heritage Program and herbarium records) were important in estimating the geographic distribution and population sizes. These data required special attention because of the diversity of persons and methods used in their collection. Records that were associated with locations at which herbarium specimens had been collected at some point in time were weighted higher than observations only.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, observations, inference, good thinking, and models must be relied on to guide our understanding of ecological relations. Confronting uncertainty then is not prescriptive. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. One element of uncertainty is the taxonomic position of *Aquilegia chrysantha* var. *rydbergii*. This situation is addressed in various sections of this assessment (see Systematics and synonymy section, Threats section, and Information Needs section).

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, employing at least two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Aquilegia chrysantha var. *rydbergii* is a regional endemic of west-central Colorado. The NatureServe (2003) Global rank for this variety of an otherwise apparently secure species is critically imperiled (G4T1Q). G4 indicates that the full species, *A. chrysantha*, is ranked apparently secure whereas T1 indicates that the variety *rydbergii* is critically imperiled. The letter "Q" is used after the T-rank to indicate that the taxon has "questionable taxonomy that may reduce conservation priority" (Nature Serve 2003). *Aquilegia chrysantha* var. *rydbergii* is designated critically imperiled (S1) by the Colorado Natural Heritage Program. The USDA FS Region 2 Regional Forester (USDA Forest Service 2003a) and the USDI Bureau of Land Management Colorado State Director (USDI Bureau of Land Management 2000) designate it a sensitive species.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Aquilegia chrysantha var. *rydbergii* occurs on land managed by the USFS, specifically the Pike-San Isabel National Forests, the Department of Defense (DoD), the BLM, the City of Colorado Springs, El Paso County, and on private land. It is listed as a USFS Region 2 sensitive species (USDA Forest Service 2003b) and is on the BLM Colorado State Director's Sensitive Species list (2000). A sensitive species indicates that it is "a plant species for which population viability is a concern as evidenced by a significant current or predicted downward trend in population number or density and/or a significant current of predicted downward trend in habitat capability that would reduce a species' existing distribution" (USDA Forest Service R2 2003b). The sensitive designation requires that a biological evaluation must be made prior to any major project, such as a timber sale, on Forest Service lands (USDA Forest Service 1995). The goal is to avoid the loss of species viability and prevent the creation of significant trends toward Federal listing (USDA Forest Service 1995). There are no plans that specifically address the management of *A. chrysantha* var. *rydbergii*. It is included in a document that outlines a general management strategy for selected sensitive plant species on the Grand Mesa, Uncompahgre, Gunnison, San Juan, Rio Grande, Pike and San Isabel national forests and Comanche and Cimarron national grasslands (USDA Forest Service GMUG, SJ-RG, PISCC1999).

El Paso County Parks and Leisure Services commissioned a survey by the Colorado Natural Heritage Program to identify sites that have potential conservation value (Doyle et al. 2001). During the survey, populations of *Aquilegia chrysantha* var. *rydbergii* were noted for Cheyenne Canyon, Bear Creek Canyon, and Cheyenne Mountain. It was particularly recommended that the population of *A. chrysantha* var. *rydbergii* in Bear Creek Canyon be given some protection from recreational developments, such as picnic areas and trails (Doyle et al. 2001). However, El Paso County does not manage the middle regions of Bear Creek Canyon where the plants are most abundant. These areas, west of Gold Camp Road, are on lands divided between the City of Colorado Springs and the Pike National Forest (USDI BLM 2000, Lieber personal communication 2003). The uppermost reaches of Bear Creek Canyon, where plants are apparently less likely to occur, are on private land. The City of Colorado Springs only considers taxa that are listed under the Endangered Species Act of 1973 when reviewing project feasibility (Lieber personal communication 2003). Therefore, the City of Colorado Springs has no plans to manage specifically for the conservation of *A. chrysantha* var. *rydbergii* (Lieber personal communication 2003).

Species that are federally listed under the Endangered Species Act are also the only species considered in development project planning on the DoD lands that contain *Aquilegia chrysantha* var. *rydbergii* (Kelso personal communication 2003). Therefore, the fate of the population at Cheyenne Mountain is subject to unpredictable land use patterns that do not consider its conservation.

At the present time, the National Forest System land on which *Aquilegia chrysantha* var. *rydbergii* occurs is managed primarily for recreation (USDA Forest Service PISCC1984). Livestock grazing is allowed in the area (USDA Forest Service PISCC 1984), but none of the allotments are currently active (Olson personal communication 2003). Some known *A. chrysantha* var. *rydbergii* sites are managed to maintain populations although their status and the management practices are not documented in writing (Olson personal communication 2003). Written documentation of plans and strategies provides a guide and a stable source of information that assures continuity during staff turnover. Further details of the sustainable management techniques that are being implemented and their efficacy are not available.

Biology and Ecology

Classification and description

Systematics and synonymy

Aquilegia is a genus of the Ranunculaceae, commonly known as the crowfoot or buttercup family (Whittemore 1997). Weber and Wittmann (2001), who place *Aquilegia* in the family Helleboraceae, follow the concept of von Vest (1818) who placed all members of the Ranunculaceae that have follicles rather than achenes into the subfamily Helleboroideae. There are approximately 70 species of *Aquilegia* (Whittemore 1997). They are generally very closely related genetically and can hybridize readily, but that there are occurrences when they don't interbreed. In fact, the barriers that separate the species have been described as being geographic rather than cytogenetic (Taylor 1967). Notwithstanding the obvious inter-fertility between species, there appears to be considerable taxonomic integrity maintained by sympatric species (Grant 1952). There was also little natural hybridization between different species of *Aquilegia* that had been planted together in rows (Anderson and Schafer 1933).

Munz (1946) recognized the close and inter-fertile nature of the straight-spurred American *Aquilegia* species that had erect blue-and-white, white, or yellow long-spurred flowers and described them as the "*caerulea-chrysantha* group." Grant (1952) remarked that the complex of yellow-spurred *Aquilegia* species, of which *A. chrysantha* is a part, appeared to represent geographical races of a single polytypic species. There are several species that have long (>3 cm) spurred yellow flowers. They include *A. chaplinei* (endemic to the Guadalupe Mountains in New Mexico), *A. hinkleyana* (endemic to Presidio County Texas), *A. longissima* (known from disjunct areas of Texas, Arizona, and northeast Mexico), *A. pubescens* (endemic to Sierra Nevada in California), and *A. chrysantha* (Grant 1952, Whittemore 1997). Following Munz's (1946) concept, Grant suggested referring to the complex of races by the name of the oldest described member, namely the *A. coerulea* group. The appropriateness of maintaining such a complex concept may need to be reconsidered. Recently, according to a critical evaluation of taxonomic characters and DNA sequence data, *A. formosa*, *A. pubescens*, and *A. shockleyi* have been identified as the most closely related species to *A. chrysantha* (Hodges 1997).

A synonym for *Aquilegia chrysantha* A. Gray var. *rydbergii* Munz is *A. thalictrifolia* (Rydberg 1902). Rydberg's *A. thalictrifolia* of southern Colorado was distinguished from *A. chrysantha* principally on the basis of smaller flower size, which was considered a poor taxonomic characteristic by Munz (1946). Munz considered a varietal position of *A. thalictrifolia* within *A. chrysantha* more appropriate. Lott (1985) proposed two additional varieties of *A. chrysantha*: variety *hinkleyana* and variety *chaplinei*. Therefore, four varieties, including the type variety *chrysantha*, are referred to in the literature. Whittemore (1997) considered that the specimens of *A. chrysantha* var. *rydbergii* he examined fell within the normal range of variation for the species *A. chrysantha*. He also followed the concept of Munz (1946), elevating the other varieties to full species status, namely *A. chaplinei* and *A. hinkleyana*.

History of species

The derivation of the name *Aquilegia* is debatable. It may be derived from the Latin *aqua*, meaning water, and *legere*, meaning to collect, because of either the wet habitat favored by some species or the quantity of liquid nectar that collects in the spurs of the flowers (Whittemore 1997). Alternatively the name may come from the Latin, *aquila* meaning eagle, because of claw shaped nectaries (Gledhill 1992).

Aquilegia chrysantha var. *rydbergii* was first collected in the mid-nineteenth century in west-central Colorado. In 1902, Rydberg originally described *A. chrysantha* var. *rydbergii* as the unique taxon, *A. thalictrifolia*. He used the epithet *thalictrifolia* because its leaves were similar to the plants of the genus *Thalictrum* (meadow-rue). However, the name *A. thalictrifolia* had already been applied to a taxon collected in Italy, and therefore it should not have been used for the Colorado taxon. Munz (1946) considered that the Colorado taxon was a variety of *A. chrysantha* and called it *A. chrysantha* var. *rydbergii*.

Non-technical description

Aquilegia chrysantha var. *rydbergii* is an herbaceous perennial with a short rootstock. It has numerous slender stems that are 20 to 120 cm tall. Towards the base, the stems are thicker and essentially hairless. Soft hairs (pubescence) cover the upper parts of the stem. The basal leaves are mostly triternate, rather thin, hairless, and light bluish-green. The yellow flowers are relatively small, the sepals being 10 to 18 mm long, the petals 7 to 12 mm long, and the nectar spurs 3.5 to 4 cm long. The stamens are exserted from the flower, and the mature styles are about 1 cm long. The fruits are derived from a single carpel that, when dry, dehisces, or splits open to release its seed, along only one side. Such a dry fruit is termed a follicle. The seeds are 1.5 to 2 mm long. This description is after Rydberg (1902) and Munz (1946). An illustration of the plant is shown in **Figure 1**, and a photograph of the whole plant and a close-up photograph of its flower are shown in **Figure 2**.

Aquilegia chrysantha var. *rydbergii* is sympatric with *A. coerulea*, which has blue and white flowers. It was reported to co-occur with *A. chrysantha* var. *chrysantha* (Ecology Consultants 1978), but this comment was unsubstantiated and *A. chrysantha* var. *rydbergii* is the only yellow-flowered taxon to occur within its range (Spackman et al. 1997). Rydberg (1906) distinguished *A. chrysantha* var. *rydbergii* from *A. chrysantha* var. *chrysantha* using a combination of several morphological characters. *Aquilegia chrysantha* var. *rydbergii* principally differs by having smaller flower size, blunter sepals, more curved follicles, and smaller and bluer leaf segments (**Table 1**). When differentiating between varieties, it may be significant that during a study of yellow-flowered *Aquilegia* populations in trans-Pecos Texas, southern New Mexico, and northern Mexico, the ratio of spur length to petal blade length was judged to be a more consistent and useful characteristic than spur length alone (Lott 1979).

References to technical descriptions, photographs, line drawings and herbarium specimens

A detailed technical description and a line drawing of *Aquilegia chrysantha* var. *rydbergii* can be found in Munz (1946). Other comprehensive technical descriptions are published in Rydberg (1902) and Weber and Wittmann (2001). A photograph and collection details of the holotype (as *A. thalictrifolia*) collected by E.L. Greene from Cañon City in 1873 are on the New York Botanical Garden Herbarium Internet site (2003). This type specimen was originally in the Herbarium at Columbia University.

Distribution and abundance

Aquilegia chrysantha var. *rydbergii* is endemic to west-central Colorado (**Figure 3**). All occurrences are within an area of approximately 60 square miles (155 square kilometers). Currently, it is known to occur in the vicinity of Cheyenne Mountain, Cheyenne Canyon (also known as Chiann Cañon and Cheyenne Cañon, and Bear Creek Canyon (also known as Bear Creek Cañon) (**Table 2**). Individuals tend to be scattered singly or in small patches of less than a dozen individuals in moist areas along creeks and side drainages. Individuals and patches can be locally abundant (Kelso personal communication 2003). In 1995, approximately 500 individuals were estimated in the Cheyenne Mountain occurrence, managed by the DoD (Occurrence 8 in **Table 2**; Kelso and DuWaldt 1995). The largest known populations are in Cheyenne Canyon and Bear Creek Canyon (Occurrences 6 and 7 in **Table 2**). Large parts of both canyons are managed by the Pike-San Isabel National Forest (**Figure 4**).

Patches distributed along a canyon are likely to interact through gene flow by pollen transfer or through seed-dispersal and therefore may be part of the same population. In this case, a population is defined as "a

Figure 1. Illustration of *Aquilegia chrysantha* var. *rydbergii* from Spackman et al. (1997). Illustration © by Janet Wingate, used with permission.

group of individuals of the same species living in the same area at the same time and sharing a common gene pool or a group of potentially interbreeding organisms in a geographic area" (National Oceanic and Atmospheric Administration 2004). In this report, the patches are referred to as sub-occurrences, and an occurrence is equated with a population. Within the known range, there are likely to be only a few populations, each of which is composed of several sub-populations. In addition, it may be that all of the plants in its relatively restricted geographic locale belong to a single, extensive metapopulation. That is, this entire range of occurrences may be linked by development, migration, and extinction of intervening sub-populations.

Approximately seven documented occurrences have been reported since 1891. Recently a single plant was discovered in Long Canyon near Boulder, Colorado (Occurrence 9 in **Table 2**). Weber and Wittmann (2001) speculate that this individual was likely an introduction from a garden in town or came from a seed mix used for revegetation of the canyon. *Aquilegia chrysantha* var. *rydbergii* has also been observed south of Cheyenne Mountain in Rock Creek Canyon (Kelso personal communication 2003). It is uncommon in this canyon, being restricted to the relatively few wet areas. It is not clear whether this occurrence extends up the canyon onto National Forest System land.

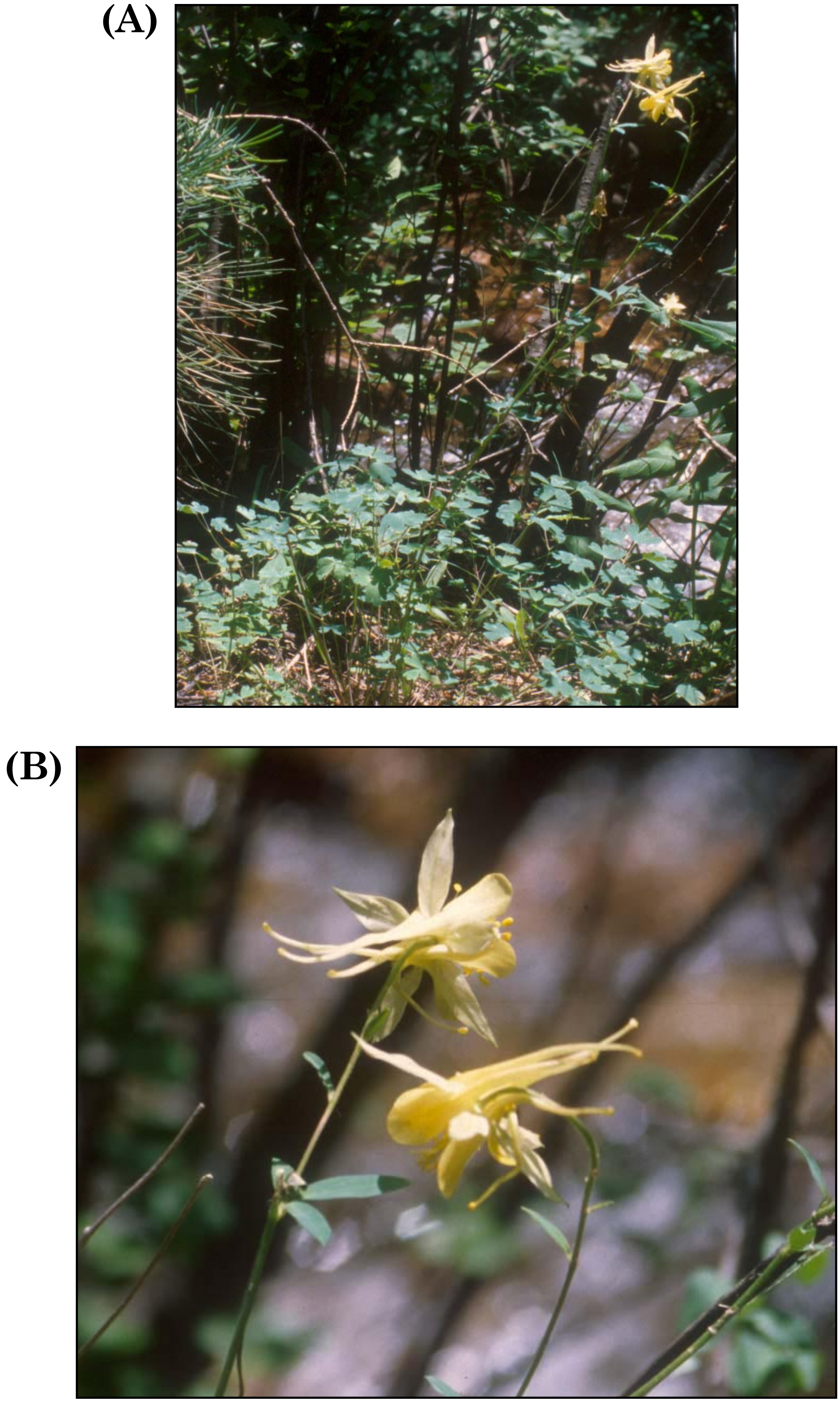

Figure 2. Photograph of (A) *Aquilegia chrysantha* var. *rydbergii* plant and (B) close-up of flower. Photographs by Juanita A. R. Ladyman.

Table 1. Differences between *Aquilegia chrysantha* var. *rydbergii* and *A. chrysantha* var. *chrysantha* (Rydberg 1906).

Aquilegia chrysantha	**Flower spur**	**Sepals**	**Follicles (dry seed pods)**
var. *rydbergii*	4 to 5 cm long	<2 cm long; ovate-lanceolate and acute in shape	Strongly curved outward
var. *chrysantha*	5 to 7 cm long	2 to 3 cm long; ovate-lanceolate to lanceolate and acuminate in shape	Almost straight

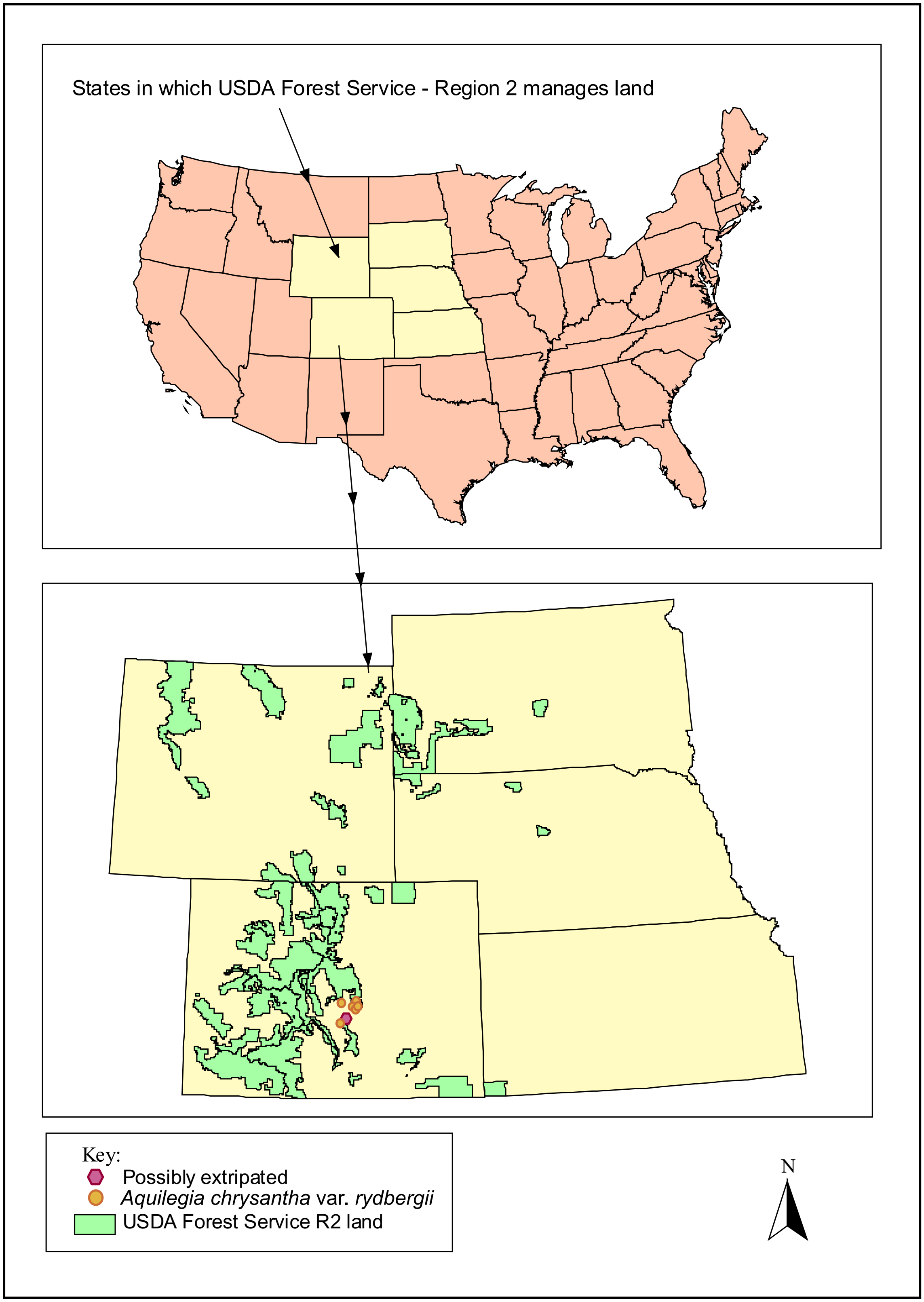

Figure 3. Range of *Aquilegia chrysantha* var. *rydbergii*.

Table 2. Occurrence data for *Aquilegia chrysantha* var. *rydbergii*.

Occurrence number	Status	Land Management	County	Observation dates	Site Location	Source of Information[1]
1	Possibly extirpated	Probably private	Fremont	June 23, 1873	Cañon City	Munz (1946)
2 (maybe same as 1)	Possibly extirpated	Unknown	Unknown	1873	Grand Canyon of the Arkansas	Rydberg (1902)
3	Unknown status	Probably private	El Paso	Summer 1889	Manitou	*Jay Steves s.n.* Summer 1889 COLO
4	Unknown status	Probably private	El Paso	July 1893	Colorado Springs	*Saunders and Alton s.n.*1893. Three specimens University of Nebraska, Lincoln Herbarium; Colorado Natural Heritage Program (2002)
5	Unknown status	City of Colorado Springs, Private land	El Paso	1885; June 5, 1879; July 13, 1906; July 1914	Chiann Cañon (1885, 1879); South Cheyenne Cañon (1906); Cheyenne Cañon (1914)	*S.B. Walker s.n.*1914 COLO; *W. Huestis s.n.* 1906 COLO. *A. Eastwood s.n.* July 1885 COLO. *M.E. Jones AM 936* 1879 COLO. Colorado Natural Heritage Program (2002)
6	Extant (2003)	Pike-San Isabel National Forest, City of Colorado Springs	El Paso	June 7, 1958; 1971; 1978; June 12, 1994; June and July 1998; July 20, 2003	Cheyenne Cañon	Colorado Natural Heritage Program (2002). Ladyman 7202003_3 2003 KHD
7	Extant (2003)	Pike-San Isabel National Forest, City of Colorado Springs, Private land	El Paso	1892; July 1935; July 1998; July 20, 2003	Bear Creek Canyon	Rydberg (1902). Colorado Natural Heritage Program (2002). Author's personal observation 2003
8	Unknown status (likely extant)	Department of Defense	El Paso	June 22, 1995	Cheyenne Mountain, NORAD site, near the north Portal	Colorado Natural Heritage Program (2002). *T. Kelso 95-1000 with J. DuWaldt* COLO
9	Most likely introduced	City of Boulder	Boulder	August 10, 1989	Long Canyon, Boulder	*T. Hogan s.n. with H. Dahnke* COLO
10	Introduced – apparently cultivated plants	Unknown	Jefferson	September 10, 2000	Denver	*S. Slaughter & T. Miller 23* CS

[1] CS: Colorado State University Herbarium
COLO: University of Colorado-Boulder Herbarium
KHD: Kathryn Kalmbach Herbarium at Denver Botanic Gardens

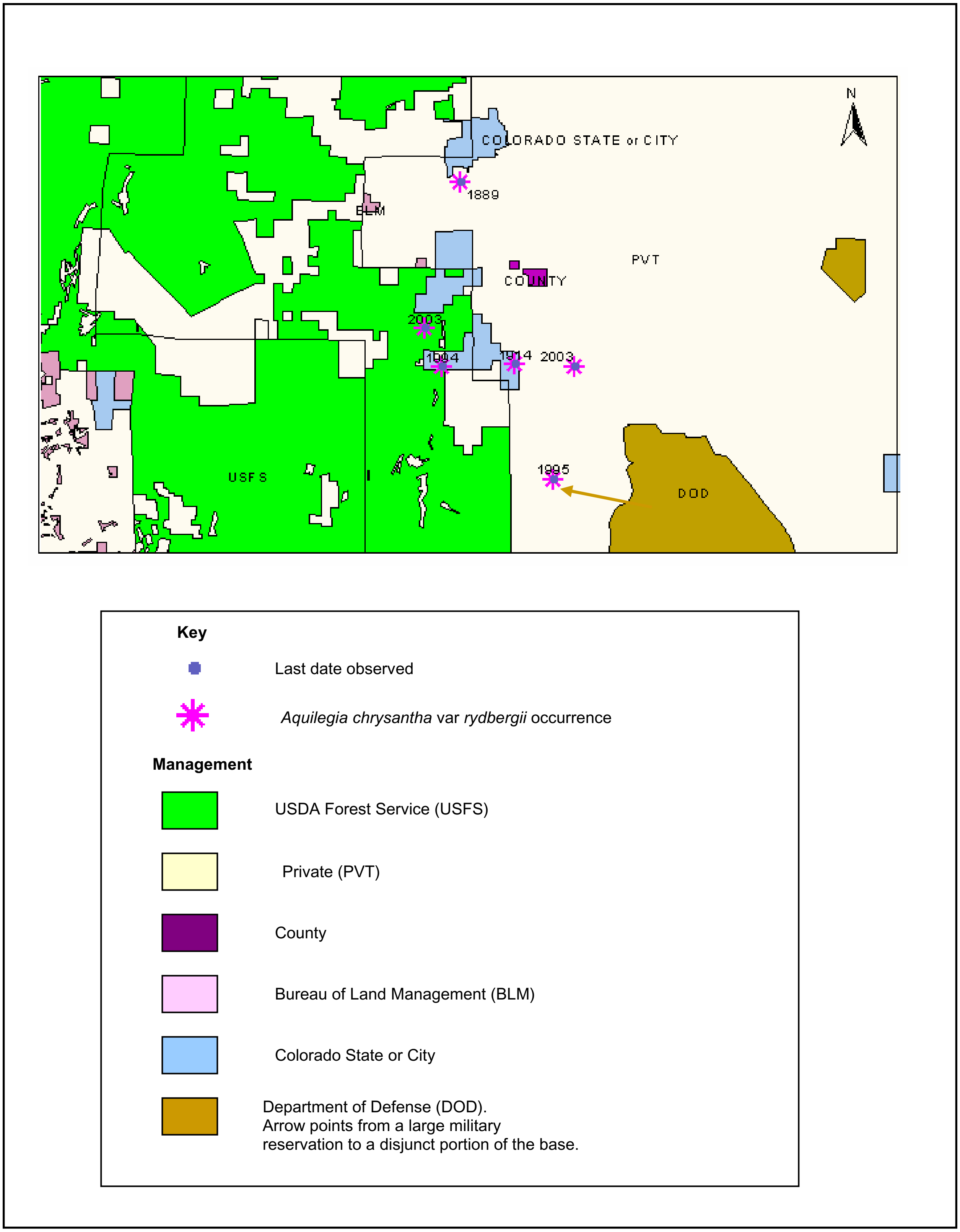

Figure 4. Overview of the land management agencies within the range of *Aquilegia chrysantha* var. *rydbergii.*

Occurrence data have been compiled from the Colorado Natural Heritage Program, specimens at the University of Colorado Herbarium (COLO), Colorado State University Herbarium (CS), the Kathryn Kalmbach Herbarium at Denver Botanic Gardens (KHD), the New York Botanical Garden Herbarium (NY), and from the literature (Munz 1946). All of the element occurrence data that are unaccompanied by herbarium specimens have to be regarded with some skepticism. Possible hybrids have been observed although they have not been confirmed (Kelso personal communication 2003, authors' personal observation 2003). There is also the possibility that *Aquilegia chrysantha* var. *rydbergii* has been mistaken for pale forms of *A. coerulea*. Very pale specimens of *A. coerulea* are apparently easy to confuse with *A. chrysantha* var. *rydbergii*, especially at a distance (Colorado Natural Heritage Program element occurrence records 2002).

It should be noted that many authors have referred to "*A. coerulea*" as "*A. caerulea*". In fact, the state flower of Colorado is described as "*A. caerulea*." However, "*coerulea*" is the original spelling (Whittemore 1997). Although several authors (see References section) may have referred to the taxon as *A. caerulea*, it will be consistently referred to as *A. coerulea* in this document.

Population trend

There are insufficient data in the literature, associated with herbarium specimens, or at the Colorado Natural Heritage Program to determine accurately the long-term population trends of this taxon. Within its range, one cannot say with certainty that *Aquilegia chrysantha* var. *rydbergii* has experienced a decline in the last century, but there has been considerable loss and fragmentation of habitat due to highway expansion, urbanization, and recreational use (Colorado Natural Heritage Program 2002). It appears that the population around Cañon City has been extirpated.

Currently, the taxon appears to be fairly abundant within the Cheyenne Canyon-Bear Canyon-Cheyenne Mountain region (Cameron personal communication 2003, Kelso personal communication 2003). Some sub-occurrences along Cheyenne Canyon may have been extirpated. For example, an occurrence was recorded in the Bear Creek Nature Center for several years prior to 1995, but no plants have been observed since 1996 (Megorden personal communication 2003). Environmental conditions might have caused, or significantly contributed to, this loss. Snowpack in the winter of 1995-1996 was substantial, and snowmelt caused considerable scouring of the river bank on which the *Aquilegia* plants were growing.

The results of a phylogeographic study by Strand and Milligan (1996) and Strand et al. (1996) of *Aquilegia chrysantha* populations in the southwestern United States are noteworthy when considering range-wide trends. They coupled genetic data, generated from chloroplast DNA analyses, with information about demography and distribution to distinguish ongoing gene flow from historical subdivision. They concluded that there was a lack of long-distance migration by seed and that natural re-colonization of sites from which populations have been extirpated is very unlikely. Their data indicate that, unless plants are artificially introduced, local extinctions are irreversible, which has obvious conservation implications.

Habitat

Aquilegia chrysantha var. *rydbergii* grows at elevations between 1,600 and 2,600 m (5,200 and 8,500 ft). It grows in organic soils and has also been observed in gravel derived from granite parent material. Often found near the base of boulders on the canyon sides and floor, it may also grow on seep-fed rocky ledges (**Table 3**). It also frequently grows along the edges of the active channel of perennial streams that may be slightly or considerably entrenched (Rosgen 1994).

Due to the consistent wetland nature of its habitat, *Aquilegia chrysantha* is designated a facultative wetland (FACW) species in New Mexico and Arizona by the USDI Fish and Wildlife Service (1988). The facultative wetland designation means that 67 to 99 percent of sample plots containing the species randomly selected across the range of the species would be classed as wetland. In contrast, *A. chrysantha* has been designated a facultative (FAC) species in Colorado, Nevada, and Utah by the USDI Fish and Wildlife Service (1988). A facultative species is equally likely to occur in wetlands or non-wetlands. For such a designation, it is estimated that 34 to 66 percent of sample plots containing *A. chrysantha* randomly selected across the range of the species would be wetland. Not withstanding this designation, moist conditions are essential for *A. chrysantha* var. *rydbergii*. It grows in shady and moist areas on slopes above a creek, along the side drainages, and within the riparian area of a perennial stream. During a survey on Cheyenne Mountain, it was noted that the plants appeared to depend on perennial water. Water was being discharged to the occurrence from higher up the mountain late in the summer even though it was a particularly dry year (Kelso and DuWaldt 1995).

Table 3. Descriptions of habitat and abundance of *Aquilegia chrysantha* var. *rydbergii* and miscellaneous comments associated with each occurrence record.

Occurrence number	Habitat	Abundance	Comments
1	No information.	No information.	Originally described as *A. thalictrifolia*.
2 (maybe same as 1)	No information.	No information.	No information.
3	No information.	No information.	Questioned leaf shape and commented that it may be cultivated. Reproductive status: Flowering. Original identification as *A. coerulea*.
4	At 6,000 ft.	No information.	No information.
5	1879: 6,000 ft. 1914: 5,750 ft.	No information.	June 1879: Reproductive status: Flowering. July 1886: Reproductive status: Flowering. July 1914: Reproductive status: Flowering. 1879, 1885, 1914: original identification *A. chrysantha*.
6	1958: On rocky cliff ledges. 1971: Below falls in canyon at 6,900 ft. 1978: Shaded foothills at 2,347 m (7,698 ft). 1994: Growing in rocks north side of falls. 1998: On both sides of the trail in coniferous forest. Along creek and up south-facing slope. 2003: Along creek in principally a Douglas-fir overstory with some aspen. Associated species included chokecherry (*Prunus virginiana*), Rocky Mountain maple (*Acer glabrum*), willow, *Mertensia* sp., *Geranium* sp., *Gallium* sp., *Thalictrum* sp. At the first site two plants of oxeye daisy (*Chrysanthemum leucanthemum*) were present.	1998: Approximately 500 plants in flower. 2003: Total 15 individuals counted. Two flowering individuals were observed approximately 0.1 miles upstream from where North Cheyenne Creek crosses highway 370. Continuing upstream for a further approximate 0.1 mile observed a patch of four individuals, two vegetative and two flowering within 1 m of each other. After approximately a further 100 m found one individual next to a boulder and two more plants within approx. 1 m of it on the other side of the trail. Walking upstream for less than 100 m counted six plants in fruit and a further isolated plant that was flowering.	1971: Specimen in flower.

Table 3 (Concluded).

Occurrence number	Habitat	Abundance	Comments
7	1935: Moist thicket. Canyon. 7,000 ft. 1998: Plants found in riparian area and on northwest-facing slopes above creek, mostly in small side drainages. Douglas-fir dominates the drainage and northwest slopes with some aspen and blue spruce. Tree cover: 20 to 60 percent. Shrubs include chokecherry, alder, willow, *Rosa woodsii*, *Ribes* sp., Rocky mountain maple, snowberry, *Juniperus communis*. Shrub cover: 10 to 80 percent. Forbs include geranium, *Poa pratensis*, *Phleum* sp., dandelion, *Mertensia* sp., *Heracleum* sp., *Thalictrum* sp., *Gallium* sp., *Potentilla* sp., *Aquilegia cerulea* [*coerulea*], *Lithospermum* sp., *Epilobium* sp., raspberry, *Fragaria* sp. Forb cover: 40 to 90 percent. Bare ground and litter cover: 30 to 80 percent. Granite gravel and granite boulders supported *A. chrysantha* var. *rydbergii* as well as more organic soil near the creek. Elevation ranged from 7,000 to 8,200 ft. 2003: Principally a Douglas-fir overstory with some aspen. Associated species included chokecherry (*Prunus virginiana*), Rocky Mountain maple (*Acer glabrum*), willow, *Mertensia* sp., *Geranium* sp., *Gallium* sp., *Thalictrum* sp.	1998: Over 100 individuals in flower counted, but those in fruit and vegetative were not easily see. Estimate at least 500 individuals. 2003: Found three plants, two on south side of stream and one on north side within 1 m of the active channel.	1998: Pale yellow flowers, sometimes difficult to distinguish from very pale forms of *Aquilegia cerulea* [*coerulea*] from a distance. Plants scattered across a large area. A well-traveled trail used by hikers, horses and bikes runs through the occurrence. Lower part of the creek includes a road and houses.
8	1995: Rocky gully with permanent waterfall. On rock steps below waterfall and east facing slopes. Soils are rock and stream channel silt and adjacent alluvial soil. 1995: Below permanent waterfall in and among granite rock faces. Elevation 7,100 ft.	1995: Several hundred plants located (population estimated at 500 individuals) including many seedlings. Most plants producing multiple flowers (estimate 60 percent flowering) and seed capsules.	1995: Habitat in excellent condition, no disease or predation noted. Plants may depend on constant availability of water (discharge from mountainside above). Alteration of surface runoff in this gully would be a threat to the population. Gully was noted to be discharging water late in summer 1994 even though that was a very dry summer. Any construction on the north side of the north portal [of the NORAD site] would impact habitat, possibly adversely.
9	Among a stand of bracken.	One plant observed, possibly introduced.	No information.
10	No information.	No information.	Cultivated.

The riparian habitat of *A. chrysantha* var. *rydbergii* is shown in **Figure 5**.

On a macro-level, the vegetation type with which *Aquilegia chrysantha* var. *rydbergii* grows is characterized as *Pseudotsuga menziesii* (Douglas-fir) forest (USDA Forest Service R2 2003a). In addition to *Pseudotsuga menziesii*, the drainages in the regions where it occurs are filled with *Corylus cornuta* (hazelnut), *Populus angustifolia* (narrowleaf cottonwood), *Betula occidentalis* (river birch), *Prunus virginiana* (chokecherry), *Acer glabrum* (Rocky Mountain maple), *Populus tremuloides* (aspen), and *Salix* spp. (willow). Tree cover ranges from 20 to 60 percent, shrub cover from 10 to 80 percent, and forb cover from 40 to 90 percent (Colorado Natural Heritage Program 2002). Grasses are a relatively small component of the community. Plant species that have been reported specifically associated with *A. chrysantha* var. *rydbergii* are listed in **Table 4**.

Reproductive biology and autecology

Aquilegia chrysantha var. *rydbergii* is a perennial taxon (Munz 1946). It reproduces primarily by seed but may spread vegetatively from slender woody rhizomes (Whittemore 1997). The earliest date that flowers have been documented by herbarium specimens is June 5th, and the latest is July 20th. The flowers are hermaphroditic, having both male and female organs.

Aquilegia chrysantha var. *rydbergii* is cross-pollinated by insects, primarily by short-tongued hawkmoths (Grant 1981, Miller 1985). The reproductive biology has not been extensively investigated in populations of *A. chrysantha* var. *rydbergii*, but *A. chrysantha* has been reported to be protandrous (Miller and Willard 1983). Protandry refers to the condition where the anthers (male organs) mature before the carpels (female organs). In protandrous, hermaphroditic species, the first flowers to open on a plant will tend to reach their female phase when later flowers are in male phase, whereas the last flowers to open will reach the female phase when no other flowers on the plant are in male phase (Brunet and Eckert 1998). Therefore, pollinators are required even for self-pollination. A study of *A. coerulea* showed it to be only partially protandrous and, in addition to between-flower self-pollination (geitonogamy), within-flower self-pollination (autogamy) was not uncommon within a population

Figure 5. Photograph of *Aquilegia chrysantha* var. *rydbergii* in Cheyenne Canyon, Pike-San Isabel National Forest. Photograph by Juanita A. R. Ladyman.

Table 4. Plant species reported to be associated with *Aquilegia chrysantha* var. *rydbergii*. This is not an exhaustive list and represents only the observations that were made on herbarium sheets, in the literature, and in Colorado Natural Heritage Program (2002).

Species	**Common name**
TREES	
Acer glabrum	(reported as) Rocky Mountain maple
Alnus sp.	(reported as) alder
Picea pungens	(reported as) blue spruce
Populus tremuloides	(reported as) aspen
Pseudotsuga menziesii	Douglas-fir
SHRUBS	
Juniperus communis	Juniper
Prunus virginiana (*Padus virginiana*) (Weber and Wittmann 2001)	(reported as) chokecherry
Ribes sp.	wild currant
Rosa woodsii	wild rose
Rubus spp.	(reported as) raspberry
Salix sp.	(reported as) willow
Symphoricarpos sp.	(reported as) snowberry
FORBS	
Aquilegia coerulea	columbine
Epilobium sp.	willow-herb
Fragaria sp.	wild strawberry
Gallium sp.	bedstraw
Geranium sp.	wild geranium
Heracleum sp.	cow parsnip
Lithospermum sp.	puccoon
Mertensia sp.	bluebells
Phleum sp.	timothy
Poa pratensis	Kentucky bluegrass
Potentilla sp.	cinquefoil
Taraxacum officinale	(reported as) dandelion
Thalictrum spp.	meadow-rue

(Brunet and Eckert 1998). A level of within-flower self-pollination (autogamy) is likely advantageous since it can provide reproductive assurance. However, between-flower self-pollination (geitonogamy) provides no such assurance (Eckert 2000).

There are no details on the quantity or viability of seed produced by *Aquilegia chrysantha* var. *rydbergii*, but some data are available for a population of *A. chrysantha* in New Mexico (Strand 1997, Stubben and Milligan 2001). Individual *A. chrysantha* plants produced from fewer than 10 to more than 100 seeds in New Mexico (Strand 1997). Seed production was closely related to environmental conditions. Plants tended to produce more seeds in years with relatively higher precipitation. Seed production was also correlated to the size of the plant. Although not invariably, plants with fewer leaves, and thus less available photosynthate, tended to produce fewer seeds. Seeds lie dormant in the seed bank (Strand 1997). The cause of the dormancy is not known, but another species of *Aquilegia*, *A. pubescens*, experiences a morphological dormancy (Baskin and Baskin 2001). In this case, the seed coat needs to be scarified, or scraped, before germination can occur.

Strand (1997) and Stubben and Milligan (2001) manipulated 10 plots of naturally-occurring *Aquilegia chrysantha* in the Organ Mountains of New Mexico to estimate the size of the seed bank, the germination rate, and the relative contributions of the seed bank and seeds released from fruits (seed rain) to new recruits. Seeds germinated from early spring through fall, and the germination rate of seed in the seed bank was estimated at 1.4 percent (Stubben and Milligan 2001). Eight-nine percent of the new recruits were derived from seed rain whereas 11 percent were from seeds in the seed bank (from data presented by Stubben and Milligan 2001).

Seed dispersal mechanisms are not known. The small, black, smooth seeds have no obvious adaptations for specialized dispersal, such as barbs that would stick to animal fur. Wind may be effective in dispersing seed although wind-dispersed seeds generally move only short distances (Silvertown 1987). Water may also disperse seeds, especially from plants growing along streams or drainages. Seed caching and dispersal by rodents and other animals may contribute to dispersal. It appears that generally seeds fall quite near the parent plants (Strand 1997, Stubben and Milligan 2001).

Demography

The seeds of *Aquilegia chrysantha* germinate and produce a rosette from which a flowering stalk develops (Stubben and Milligan 2001). The rosette will have died by the following year, but another rosette develops on the caudex, usually under the old rosette (Stubben and Milligan 2001). Plants are thus iteroparous, reproducing for a number of years before they die. Older plants may have more than five rosettes, each producing a flowering stalk (Stubben and Milligan 2001). Plants can become dormant for at least one year during times of environmental stress. The caudex, or woody stem, serves as the organ of dormancy, and no rosettes are produced during a dormant year (Strand 1997). Species having organs that experience prolonged dormancy are not unusual amongst many genera of geophyte vascular plants (Lesica and Steele 1994). In cultivation, *A. chrysantha* is reported to be particularly long-lived, relative to other species of *Aquilegia* (Munz 1946). Most records suggest that the majority of *A. chrysantha* var. *rydbergii* plants are either flowering or with fruit. Few vegetative plants have been reported. Seedlings have only been reported in the Cheyenne Mountain occurrence, where they were numerous (Kelso and DuWaldt 1995). It is not clear whether the general absence of seedlings is due to their being small and inconspicuous or actually due to rarity. It is likely that they are easily overlooked because of the abundance of other vegetative groundcover in the areas where they grow. In addition, during casual observation, their leaves may be mistaken for *Thalictrum* species, which are very common within their habitat.

Although there are no demographic studies of *Aquilegia chrysantha* var. *rydbergii*, several years of demographic data have been collected on *A. chrysantha* in the Organ Mountains of New Mexico. The fates of 2,152 plants were followed over the six years of study (Stubben and Milligan 2001). Plant loss from herbivores and unknown causes during the first two years of the study was approximately 10 percent (Strand 1997). In some other years, losses were higher (Stubben and Milligan 2001). Size classes rather than age classes were used in developing a stage projection model after the method of Lefkovitch (1965). A lifecycle diagram for *A. chrysantha* var. *rydbergii* is given in **Figure 6**. It is based on the results of Stubben and Milligan (2001). Strand (1997) reported that seeds that had over-wintered at least once germinated from the seed bank. It was estimated that the seed bank might be depleted in five years if seed production ceased (Stubben and Milligan 2001).

The equilibrium growth rate (λ) integrates the effects of survival, growth, and fecundity of the different life history stages into a single parameter and is useful in describing critical stages in life histories (Caswell 1989, Silvertown et al. 1993). When λ equals one, the population is stable; when it is less than one, the population is in decline; when it is greater than one, it is growing (Mills et al. 1999). Strand (1997) calculated λ from transition matrices over 1995 to 1996 and 1996 to 1997 (**Table 5**). The 1995 to 1996 period was marked by drought whereas the 1996 to 1997 period was relatively wet. Values of λ indicate that the population was in decline the first year but grew in the second year when there was adequate precipitation. The estimate of λ (0.7) derived from multiplying the matrices from individual years and then calculating λ from the product matrix over the three-year period indicates a population in decline. Stubben and Milligan (2001) extended this study for years 1997 to 1998, 1998 to 1999, and 1999 to 2000 (**Table 5**). As during the first three years of study, considerable variation that was closely linked to precipitation existed between years. Considering all six years (five transition periods), although both the mean and product matrices project λ to be less than 1, when λ was calculated from a weighted mean matrix it was 1.02. These results may suggest a fundamentally stable population that may be vulnerable to environmental perturbation.

Elasticity analyses were made for each transition period (Strand 1997). Elasticities predict the proportional change in growth rate given a proportional change in a matrix element while all other elements remain constant (Mills et al. 1999). In both periods

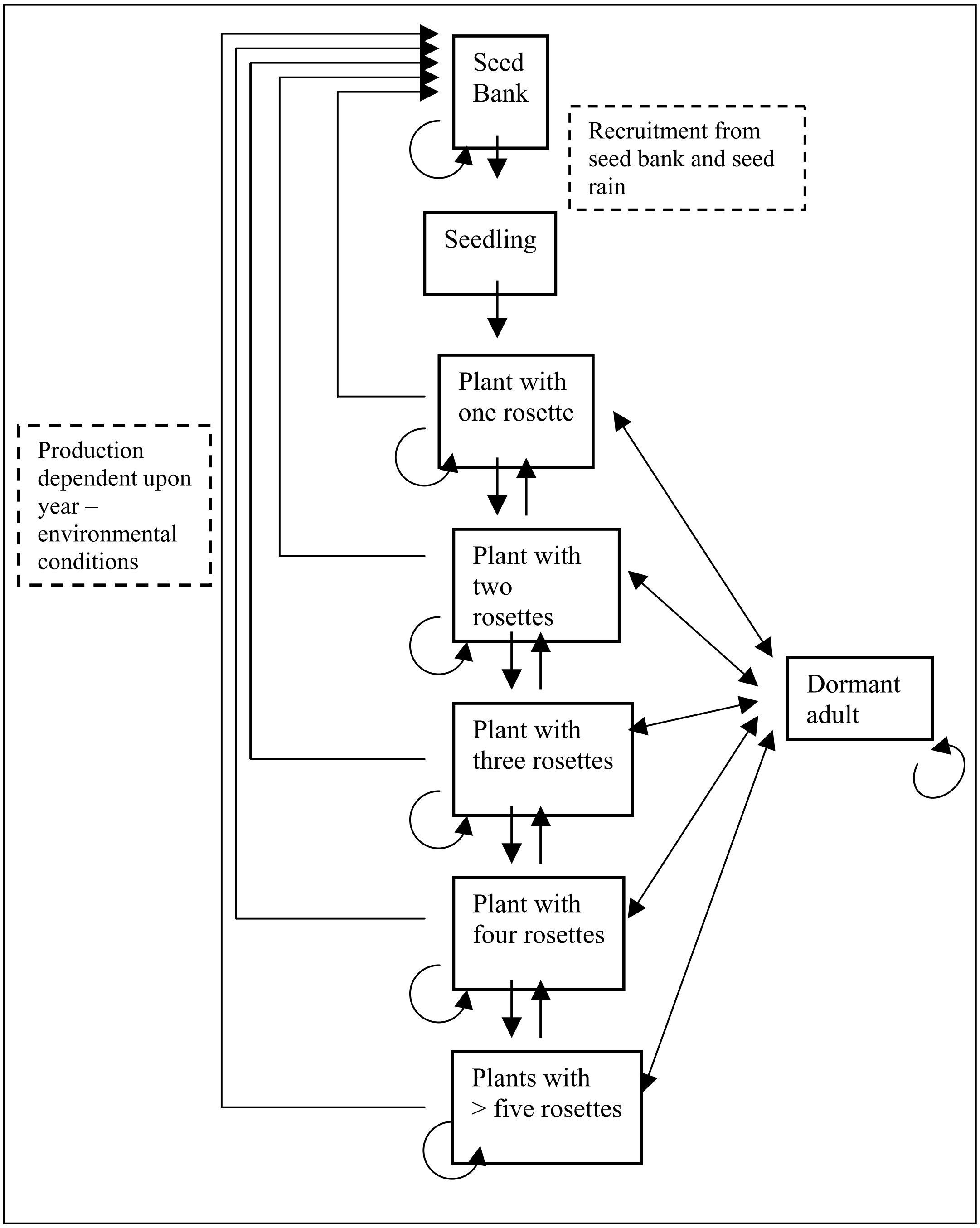

Figure 6. Lifecycle diagram for *Aquilegia chrysantha* var. *rydbergii* (after Strand 1997 and Stubben and Milligan 2001).

Table 5. Estimates of population equilibrium growth rate for *Aquilegia chrysantha* from annual matrices, and the growth rate calculated from the mean, weighted mean, and product matrix (from Strand 1997 and Stubben and Milligan 2001).

Transition matrix	Population equilibrium growth rate (λ)
1995 to 1996	0.46
1996 to 1997	1.72
1997 to 1998	0.96
1998 to 1999	1.03
1999 to 2000	0.67
Mean	0.96
Weighted mean	1.02
Product	0.54

(1995 to 1996 and 1996 to 1997) the highest elasticity is in the persistence of the medium-sized plants. That is, persistence of medium-sized plants was a significant contributor to λ. Elasticities were high for recruitment from the seed bank into medium sized plants in the 1995 to 1996 period and into small and medium-sized plants in the 1996 to 1997. Seed production by medium-sized plants from 1995 to 1996 and by all sizes of plants from 1996 to 1997 also had significant elasticity values.

The adult plant and its rootstock are thus apparently important stages in the life cycle of *Aquilegia chrysantha*. In addition, elasticity analyses indicated that seed production and seedling recruitment might also be critical in some years. Species having a similar life form and regenerative strategy were characterized as a stress tolerant-competitor by Grime et al. (1988), and as a K-selected species, which are those that have a long life span in relatively stable habitats, by MacArthur and Wilson (1967).

The year-to-year variability in growth rate emphasizes the potential inaccuracy of making predictions using limited information. These studies indicated that individual fecundity and development as well as population size were very sensitive to current environmental conditions. While these data can provide some valuable insights into the life history and ecological requirements of *Aquilegia chrysantha* var. *rydbergii*, it must be cautioned that they may also be misleading. These data were generated in the Organ Mountains of New Mexico, which are environmentally different to the Cheyenne Canyon region in Colorado. In addition, the genetic differences between the plants in New Mexico and those in Colorado may also be sufficient to invalidate extrapolation.

Information on other *Aquilegia* species suggests that there is the potential for both hybridization and inbreeding depression among *A. chrysantha* var. *rydbergii* populations. Interspecific hybridization among *Aquilegia* species is common (Taylor 1967). Hybrids are often reported in nature. A likely hybrid between *A. coerulea* and *A. chrysantha* has been found within the range of *A. chrysantha* var. *rydbergii* (Kelso personal communication 2003; land ownership and exact location unspecified). Hybrid specimens need to be confirmed, and the frequency of hybridization should be explored further. Pollinator preference, differences in flower structure, and/or spatial separation of different species may contribute to genetic isolation of the parents and hybrid progeny (see Community ecology section).

Self-pollination in *Aquilegia chrysantha* var. *rydbergii* may lead to populations experiencing inbreeding depression. Inbreeding depression is deleterious because, as the name implies, the consequence is that a plant experiences a lack of fitness due to weakness in some aspect of its physiology. For example, its germination, its competitive ability, its over-wintering ability, or its reproductive effort may be compromised in some way. Inbreeding depression may be due to deleterious recessive or partially recessive alleles, which are masked at heterozygous loci by dominant alleles, becoming fully expressed in homozygotes or, alternatively, alleles may interact in an over-dominant manner, such that the fitness of either type of homozygote is lower than that of heterozygotes (Dudash and Carr 1998). Some studies have suggested that *A. coerulea*, another protandrous hermaphroditic species, might suffer from considerable inbreeding depression due to selfing (Montalvo 1994).

More recent research by Brunet and Eckert (1998) suggested that inbreeding depression was negligible in *A. coerulea*. However, the variation in the condition among populations was high, which suggests that some populations, especially smaller-sized ones, may be at risk. The propensity for inbreeding depression may be mitigated by substantial levels of outcrossing, indicating the importance of pollinators for sustainable populations. Studies on *A. coerulea* indicated that approximately equal amounts of selfing and outcrossing occurred (Brunet and Eckert 1998). Although these studies were made on *A. coerulea*, the demographic and genetic similarity between species likely makes consideration of the observations appropriate for *A. chrysantha* var. *rydbergii*.

Community ecology

Members of the Ranunculaceae are often poisonous, but the herbage of *Aquilegia chrysantha* does not appear to be particularly toxic. There is little information about secondary plant compounds in *A. chrysantha* and no information on *A. chrysantha* var. *rydbergii* specifically. The Miwok Native Americans boiled and ate the young leaves of *A. formosa*, a closely related species, in the spring (Moerman 1998; see Systematics and synonymy section). The palatability of *A. canadensis* is rated fair for sheep, poor for cattle, and non-palatable for horses (Dayton 1960). Although the roots and leaves of several species appear to contain pharmacologically active compounds, the seeds of most *Aquilegia* species appear to be the richest in such compounds (Moerman 1998). The seeds of some species are also reported as toxic (Tampion 1977, Woodward 1985). Caching and dispersal of seeds by rodents and other animals may be unlikely if *A. chrysantha* var. *rydbergii* seeds are toxic (see Reproductive biology and autecology section).

Aquilegia species are cross-pollinated (Miller and Willard 1983). The flower color and the length, shape, and orientation of the nectar spurs influence the types of pollinator species (Hodges 1997). Red-flowered *Aquilegia* species are primarily pollinated by hummingbirds, pale-colored and yellow-flowered *Aquilegia* species such as *A. chrysantha* by hawkmoths, and blue-flowered *Aquilegia* species by bumble-bees (Clausen 1951, Grant 1952, Miller and Willard 1983, Miller 1985, Grant 1981). This distinction among pollinators may contribute to genetic isolation in sympatric species in some areas (Grant 1952, Hodges 1997). However, this generalization is not inviolate. In Colorado, hummingbirds, sphinx moth, and several species of bumblebees have been observed visiting *A. coerulea* although not all within the same populations (Grant 1976, Miller 1978). In addition, Chase and Raven (1975) noted that hawkmoths, hummingbirds, and bumblebees all visited both *A. formosa* (red-flowered) and *A. pubescens* (yellow-flowered). In this case, they concluded adaptation to different habitat, and thus spatial separation, was likely the most important factor in maintaining genetic uniqueness between the two species. Parents and hybrid progeny of several species of plants may be separated by several other methods. For example, temporal difference in the flowering period reduces the hybridization potential of two southwestern *Oenothera* species. Although both are pollinated by solitary bees, hybrids are rare because flowers of one species open before sunrise and are visited by early morning bees whereas those of the other species open late in the afternoon and are visited by bees with afternoon activity (Raven 1962). In addition, different structural characteristics of the flower, such as the floral tube length, can also prevent effective pollen transfer between species (Grant 1981). That is, although potential pollinator-visitors are the same for all species in a given area, differences in flower structure prevent effective pollen transfer.

Although *Aquilegia chrysantha* var. *rydbergii* is well adapted for hawkmoth pollination (Grant 1952, Lott 1979) and the long spurs may exclude other pollinators from nectar, a less restricted assemblage of pollen vectors may be most advantageous. In some years or local weather conditions, hawkmoths appear to be unreliable pollinators. The annual numbers of hawkmoths fluctuate considerably due principally to weather conditions and the amount of herbaceous material available to their larvae (Casey 1976, Miller 1978). Their flight is also related to evening temperature. Hawkmoths are less inclined to fly on cool evenings (Stockhouse 1973).

Bell (1969 in Lott 1979) studied *Aquilegia elegantula* and *A. coerulea* and their pollinators in Colorado. He found that *A. elegantula*, which was primarily pollinated by hummingbirds, showed very little floral variation. In contrast, in the same area *A. coerulea*, which is primarily pollinated by hawkmoths, showed marked variation in floral morphology. He concluded that the variation in *A. coerulea* was not attributable to hybridization between the two species. There was a difference in pollinator abundance. Whereas hummingbirds were common, hawkmoths were scarce and *A. coerulea* was promiscuously pollinated by flies, beetles, and other non-specialist arthropods. Bell hypothesized that the ability of *A. coerulea* to rely on less specialized pollinators reduced selection pressures on the adapted floral parts and allowed greater floral variability in *A. coerulea* (Lott 1979). Whether this is the case or whether floral variability is the reason for the less restrictive assemblage of pollinators, it is still an interesting observation on the mutualism that exists between pollinators and plants. One may speculate that differences in local arthropod communities contribute to the considerable variability among western populations of *A. chrysantha*.

There is no information on mycorrhizal associations with *Aquilegia chrysantha* var. *rydbergii*. Reports of an association between *A. canadensis* and vesicular-arbuscular mycorrhizae are contradictory (Sullivan 1992, Dawson and Ehleringer 1993). It is possible that environmental (edaphic) conditions affect the association.

There have been no critical surveys of the plant associations with *Aquilegia chrysantha* var. *rydbergii*. The available information suggests that in Bear Creek Canyon and in the mid- to upper parts of Cheyenne Canyon in the Pike-San Isabel National Forest, it is a member of the *Pseudotsuga menziesii*/*Betula occidentalis* (Douglas-fir/river birch) woodland association (Casey et al. 2003). This plant association appears to be limited to perennial streams where the cold-air drainage and perennial stream flow provide a cool and moist environment that supports a diverse shrub canopy (Casey et al. 2003). Occurrences lower in Cheyenne Canyon are likely to merge into a *Picea pungens* (blue spruce) association (Casey et al. 2003). In moist canyon bottoms, it is not unusual for *Pseudotsuga menziesii* to co-dominate with *Picea pungens* (Colorado Division of Wildlife 1996) Since these associations are in late-seral stages, it would take a long time to regenerate a similar community structure if substantial modification to the abundance of the dominant species occurred (Rondeau 2001).

Local microhabitat conditions may also be very important to *Aquilegia chrysantha* var. *rydbergii*. Within an occurrence, it grows singly or in patches along a creekside or drainage, leaving much of an area unoccupied. Moisture, inter- or intra- species competition, light (canopy cover), and soil conditions may all contribute to its patchy distribution. Canopy cover, specifically the understory light environment, was a single parameter that was hypothesized to influence population size of yellow-flowered *Aquilegia* species in west Texas and New Mexico (Gallagher and Milligan 2001). Some traits, specifically number of flowers, number of fruits, leaflet width, number of leaves, stem height, and number of rosettes, appeared to be influenced by canopy cover, but the degree to which the traits were correlated depended upon the population. At a population level, canopy cover that ranged from approximately 25 to 73 percent did not appear correlated to population size *per se* (Gallagher and Milligan 2001). Since canopy cover appears to influence the organs that are ultimately responsible for population development, it would be interesting to re-evaluate the populations in a decade or so. Canopy cover was not considered in relation to the spatial distribution of individuals within populations.

An envirogram is a graphic representation of the components that influence the condition of a species and reflects its chance of reproduction and survival. Envirograms have been used to describe the conditions of animals (Andrewartha and Birch 1984) but may also be applied to describe the condition of plant species. Those components that directly impact *Aquilegia chrysantha* var. *rydbergii* make up the centrum, and the indirectly acting components comprise the web (**Figure 7** and **Figure 8**). Much of the information to make a comprehensive envirogram for *A. chrysantha* var. *rydbergii* is unavailable. The envirogram in **Figure 7** is constructed to outline some of the resources that are known to impact the species directly and also includes some more speculative factors that can be tested in the field by observation or by management manipulation. Dotted boxes indicate the resources, such as shade, that are of a speculative nature. There is a lack of direct studies on this species that leads to the stretching of the significance of observations and forming opinions from inference rather than fact. Inferences must be tested and are dangerous to use in predicting responses to management decisions.

In summary, resources include surface water or at least damp conditions that provide a suitable moist environment (see Habitat section). Shade is included in the envirogram in a dotted box because open canopy with adequately moist conditions may be just as appropriate. Pollinators for cross-pollination are important. Water, rodents, arthropods, and wind may be agents of seed dispersal. All components of climate, most easily separated into temperature and precipitation, influence the population size of both plants and pollinators.

CONSERVATION

Threats

Threats and potential threats that have been identified are related to habitat loss, principally by human recreation and herbivory, interspecific plant

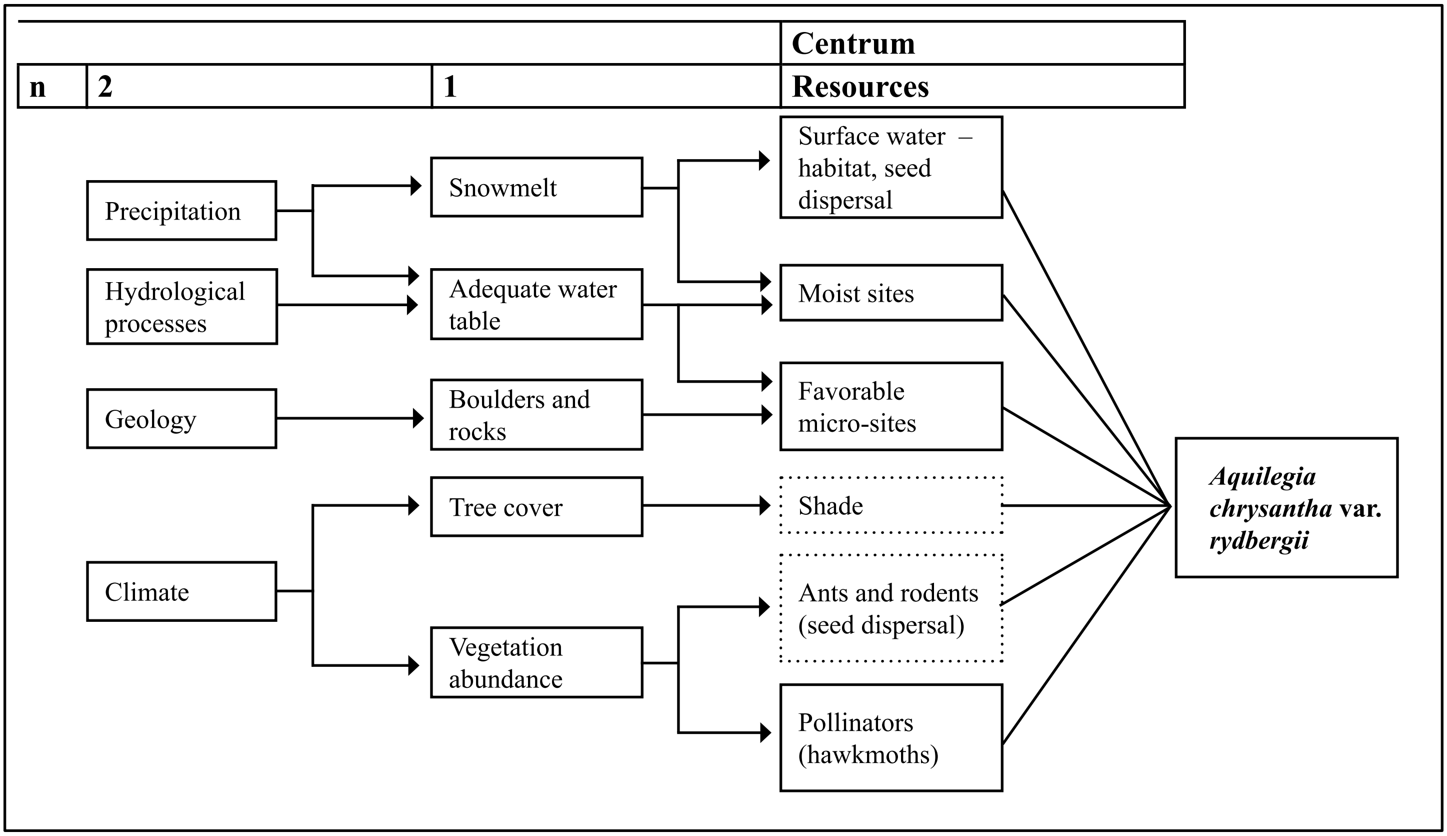

Figure 7. Envirogram outlining the resources of *Aquilegia chrysantha* var. *rydbergii*.

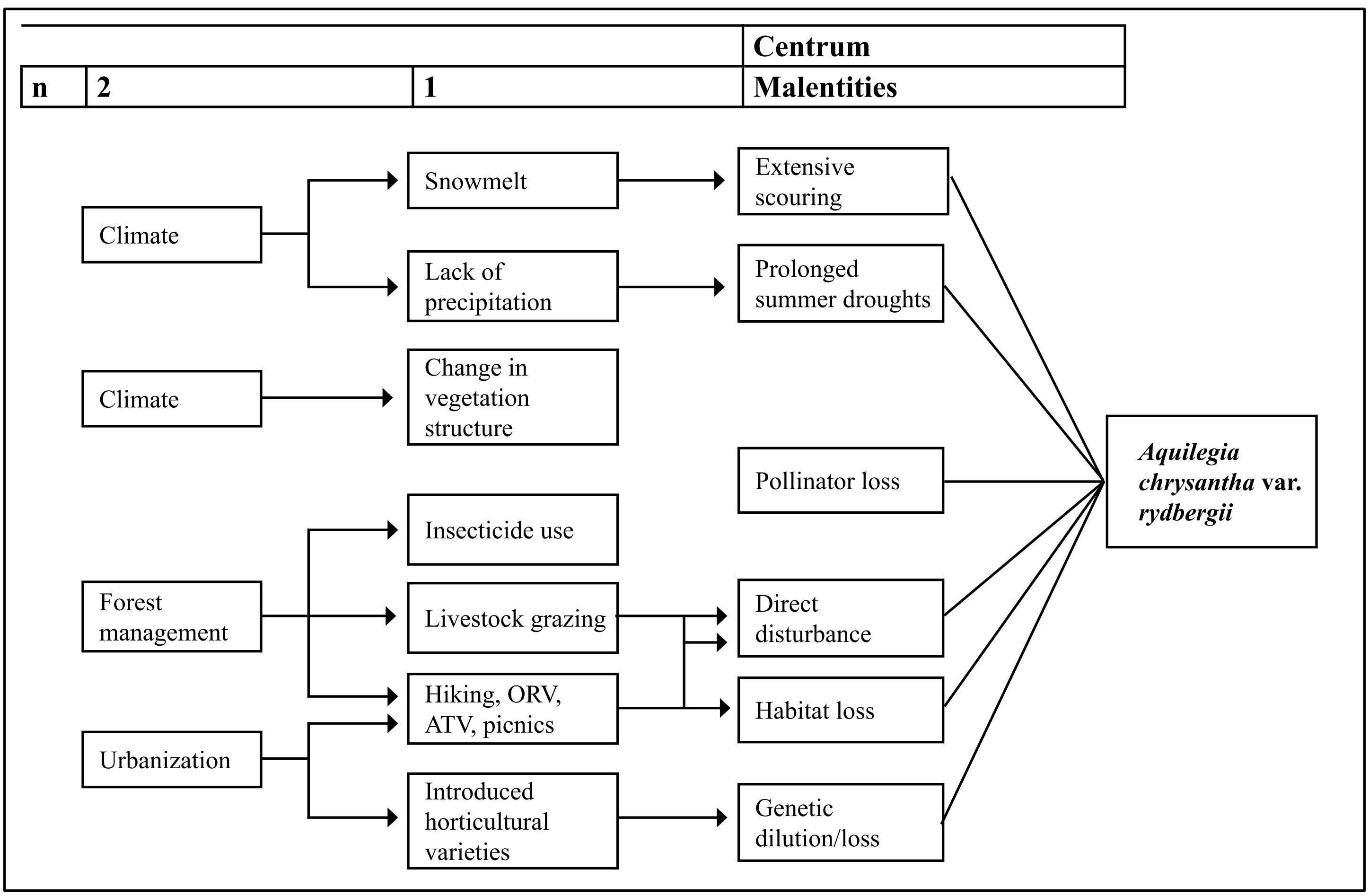

Figure 8. Envirogram outlining threats and malentities to *Aquilegia chrysantha* var. *rydbergii*.

species competition, and environmental stochasticity. Some of these factors were alluded to in the Community ecology section. The range of *Aquilegia chrysantha* var. *rydbergii* is under mixed management, but all areas appear to face similar threats. Each threat or potential threat is discussed briefly in the following paragraphs.

Habitat loss appears to be a substantial concern (Doyle et al. 2001). Parts of two areas where it occurs, Bear Creek Canyon and Cheyenne Canyon, are managed by the Pike-San Isabel National Forest. Bear Creek Canyon is apparently less used at the present time because there are limited points of access (Doyle et al. 2001). The North Cheyenne Canyon/Stratton Open Space area and the Bear Creek Canyon Park are, respectively, west and northwest of the Pike-San Isabel National Forest land. The City of Colorado Springs manages these parks primarily for recreation (Lieber personal communication 2003). All known occurrences on the Pike-San Isabel National Forest fall within Management Area type 2A where the "management emphasis is for semi-primitive motorized recreation opportunities, such as snowmobiling, four wheel driving and motorcycling both on and off roads and trails. Range resource management provides sustained forage yields" (USDA Forest Service PISCC 1984).

Cheyenne Canyon is readily accessible and is currently a popular recreation area (for example see "Climbing boulder" and "Online Highways" Internet sites listed in the References section). The trail at the upper end of North Cheyenne Creek is open to motorbikes (Doyle et al. 2001). Trail widening and use of the riparian zone for picnics are considered current threats in Bear Canyon Park and the North Cheyenne Canyon Open Space (Doyle et al. 2001). These concerns likely apply to National Forest System land. A well-used hiking trail on Pike National Forest land goes through *Aquilegia chrysantha* var. *rydbergii* habitat near the creek. Intensive trail use has increased erosion, which not only increases trail size but may eventually increase sediment deposition in the streams. Sediment deposition has unpredictable consequences on streamside populations of *A. chrysantha* var. *rydbergii*. Small increases over a long period may not have substantial impact on the plants as they grow on the banks of the streams and their root systems may actually benefit from fractionally more soil build up. Southern populations of *A. chrysantha* reportedly have strong and vigorous root systems (Lott 1979). However, copious sediment deposition may bury seeds and roots so deeply that they are unable to sprout. Another aspect of increased sediment deposition that has unknown consequences is the alteration of the nutrient dynamics of the system.

Another consideration that is linked to high recreational use of occupied habitat is the incidental collection of the taxon. *Aquilegia chrysantha* var. *rydbergii* has an ostentatious and attractive flower. Fortunately this does not appear to be an imminent problem (Olson personal communication 2003). However, the potential impact of collection on seed set and long-term abundance throughout the recreational areas where it occurs has not been evaluated. It is unlikely that the popularity of Cheyenne Canyon and nearby areas for recreation will decline in the foreseeable future. It is more likely that use will increase as the human population grows in the nearby urban areas of Colorado Springs, Manitou Springs, and Broadmoor. El Paso county experienced a 30.2 percent increase in the human population between 1990 and 2000, having a population of 516,929 by 2000 (U.S. Census Bureau 2001). Although the rate of population increase may slow, it is unlikely to stop.

Herbivores may impact *Aquilegia chrysantha* var. *rydbergii* plants through consumption. Direct trampling by large mammalian herbivores is also likely to disturb plants and their habitat. Currently there is no active livestock grazing on National Forest System land occupied by *A. chrysantha* var. *rydbergii*, but if priorities change this may become a concern (USDA Forest Service PISCC 1984; also see Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies section in this document). Disturbance that results in plant losses from any source may be of significant concern because elasticity analysis of a population of *A. chrysantha* suggested that the persistence of medium-sized adults is important to the population sustainability (see Demography section). Because seed is likely dispersed only short distances, the value of the seed bank must be substantial for sustained populations. However, the seed bank will also be impacted by accelerated erosion that accompanies direct disturbance.

There is private land in the upper regions of Bear Creek Canyon and in small enclaves in Cheyenne Canyon. Private houses are quite numerous in the area, and there is the potential for more to be built. As urbanization encroaches within pollinator range of its natural habitat, introduction of horticultural species may become a concern. Many horticultural varieties of *Aquilegia chrysantha*, as well as other *Aquilegia* species and hybrids, are available in the horticultural trade. As the human population grows in areas within its habitat, chance introduction of other *A. chrysantha* genotypes is not a remote possibility. Another related threat is chance introduction of non-local, if not non-native, *Aquilegia* species through seed mixes used in re-vegetation projects (see Distribution and abundance section and Community ecology section). The potential threat from loss of genetic integrity by hybridization with naturally sympatric species cannot be estimated without more information on the frequency of hybridization or pollination systems. Potential hybrids have been reported but not confirmed within the range of *A. chrysantha* var. *rydbergii*.

The consequences of forest thinning are not clear. *Aquilegia chrysantha* var. *rydbergii* is commonly reported in shady conditions, but moist habitat in a relatively open canopy may be appropriate (see Community ecology section). Therefore, a conservative approach would be to limit such activities while evaluating the consequences of any thinning practices by monitoring for several years before and after treatments are made.

The effect of other types of disturbance, such as fire, on this species is also unknown. *Aquilegia chrysantha* var. *rydbergii* is likely adapted to fire as it has evolved in forested regions. On the other hand, one may speculate that its moist habitats infrequently experience hot fires and may to some extent provide refugia from light fires. Seed in the seed bank, rather than dispersed by seed rain, may be very important to population recovery after fire (see Reproduction biology and autecology section).

Aquilegia chrysantha var. *rydbergii* may be vulnerable to declines in pollinator populations or to changes in species composition of pollinator populations. Pollinators are important because facilitated autogamy, geitonomy, and a certain level of cross-pollination are likely important for adequate seed set and population sustainability (see Reproductive biology and autecology section and Demography section). Pesticide applications, made to control arthropod pests related to other management issues, may negatively affect pollinator assemblage and abundance in the region. For example, control of western spruce budworm (*Choristoneura occidentalis*), which is a pest of *Pseudotsuga menziesii* as well as other conifer trees, may become desirable because acreages of *P. menziesii* with light and moderate defoliation are increasing in the Front Range of El Paso and Douglas counties (Harris 2002). In addition, habitat alteration and fragmentation and the introduction of non-native plants and animals all contribute to reducing pollinator population sizes as well as to causing the extirpation or extinction of individual pollinator species (Bond 1995).

Non-native invasive plant species (i.e., weeds) may be a substantial threat to *Aquilegia chrysantha* var. *rydbergii*. Because this species has evolved in a relatively well-vegetated environment, it may be moderately competitive but its vulnerability will depend upon the invading species. To its disadvantage, *A. chrysantha* var. *rydbergii* is not strongly rhizomatous and does not appear to grow rapidly. In addition, many noxious weed species secrete allelopathic chemicals into the soil that also contribute to habitat loss (Sheley and Petroff 1999). Herbicides are generally applied to control the spread of weeds, but many of these will directly impact *Aquilegia* species as well as the target plants. A native of Eurasia, oxeye daisy (*Leucanthemum vulgare* previously known as *Chrysanthemum leucanthemum*), has been found growing within a meter of *A. chrysantha* var. *rydbergii* in Cheyenne Canyon on the Pike National Forest (author's personal observation 2003). Oxeye daisy is designated a noxious weed in the State of Colorado (Colorado Department of Agriculture 2001, Colorado Department of Agriculture undated).

As well as direct and indirect threats associated with human activities, there are uncertainties that can only be addressed by increasing both the number of populations and their sizes. These uncertainties, which are typically addressed in population viability analysis, include elements of environmental stochasticity, demographic stochasticity, genetic stochasticity, and natural catastrophes (Shaffer 1981). Population viability analysis has not been addressed for *Aquilegia chrysantha* var. *rydbergii*, and a viable minimum population size cannot be estimated from available data. However, where occurrences of this taxon are small, such as less than 50 individuals, demographic stochasticity may be important (Pollard 1966, Keiding 1975). That is, chance events independent of the environment may affect the reproductive success and survival of individuals that, in such small populations, have a proportionally more important influence on survival of the whole population. In addition, the consequences of inbreeding depression, relating to both genetic and demographic stochasticity, may become a significant threat if populations experience significant declines in size and number due to habitat loss, direct destruction, or attrition due to poor reproductive output (see Demography section).

Natural catastrophes and environmental stochasticity appear to pose significant threats to

Aquilegia chrysantha var. *rydbergii*. Global climate change that is associated with drying conditions may adversely affect this taxon. In the last 100 years, the average temperature in Fort Collins, Colorado has increased 4.1 °F (2.3 °C). Based on projections made by the Intergovernmental Panel on Climate Change and results from the United Kingdom's Hadley Centre's climate model (HadCM2), by 2100, temperatures in Colorado could increase by 3 to 4 °F (1.6 to 2.2 °C) in spring and fall, with a range of 1 to 8 °F (0.5 to 4.4 °C), and 5 to 6 °F (2.7 to 3.3 °C) in summer and winter with a range of 2 to 12 °F (1.1 to 6.6 °C) (U.S. Environmental Protection Agency 1997). *Aquilegia chrysantha* appears to be very sensitive to environmental variation (Strand 1997). A series of drought years are predicted to lead to extinction of populations in the Organ Mountains (Strand 1997). Some climate change models, such as HadCM2, have suggested that future snowfall may be higher than historically average. This may mitigate the drought scenario, but a warmer climate would lead to earlier and more intense spring snowmelt. High instream flows in spring may contribute to extensive scouring and local extirpation of some creek side patches of *A. chrysantha* var. *rydbergii*. Compounding the effects of long-term drought is the potential for permanent changes in the hydrology of the area. Hydrology may be impacted if water requirements increase through increased urbanization or by developments on a nearby military base.

In summary, threats, or malentities, tend to be interrelated and are outlined in the envirogram in **Figure 8**. Habitat loss appears to be a significant concern and may be caused directly by anthropogenic activities or by invasive weeds. Populations on National Forest System land, as well as on adjacent lands managed by the City of Colorado Springs and El Paso County, are likely to be most vulnerable to activities associated with recreation and invasive weeds encroaching habitat. Horses and vehicles, including all-terrain vehicles, dirt bikes, and off-road vehicles, will contribute to the spread of invasive weeds. Livestock grazing, particularly trampling, is a potential threat on National Forest System land. Above average snowfall that results in high instream flows may cause scouring along the active channel and may remove vulnerable occurrences. Conversely, a drought lasting through multiple years appears to be potentially even more detrimental (see Demography section). Although, there is little, on a local level, that can be done to avoid the consequences of the threat of global climate change, control of pressures, for example preventing accelerated erosion, that contribute to stress may to some extent mitigate the impacts.

Conservation Status of the Species in Region 2

Aquilegia chrysantha var. *rydbergii* has apparently been extirpated from the sites found in the late 1800s (1873 to 1893) in the Cañon City area. There is no evidence to support or to refute the hypothesis that the abundance of this taxon is significantly changing within the Cheyenne Canyon and Bear Creek regions, which are primarily managed for recreation at the present time (see Threats section; USDA Forest Service PISCC 1984, Doyle et al. 2001, Lieber personal communication 2003). As of 2003, *A. chrysantha* var. *rydbergii* is reported as being locally abundant in some regions of Cheyenne Canyon on National Forest System land (Cameron personal communication 2003). Anthropogenic activities have led to a loss of habitat, but the cumulative impact on the abundance and distribution of *A. chrysantha* var. *rydbergii* cannot be accurately estimated. The Colorado Natural Areas Program and the Colorado State Parks Department have recently established Cheyenne Mountain State Park within the geographic range of *A. chrysantha* var. *rydbergii*. Although this park includes areas with ostensibly suitable habitat for *A. chrysantha* var. *rydbergii*, no plants have been observed (Fenwick 2001). Potential habitat for this taxon has not been rigorously defined. Potential habitat can best be described as habitat that, from casual observation, appears suitable for the taxon, but which is not occupied by it.

Management of the Species in Region 2

Implications and potential conservation elements

Whittemore (1997) considers that the characteristics of specimens of *Aquilegia chrysantha* var. *rydbergii* that he examined fall within the normal range of variation of *A. chrysantha*. *Aquilegia chrysantha* is a relatively widespread taxon, being reported from Arizona, New Mexico, Texas, Utah, and Colorado in the United States and from northeastern Mexico. It is understood to be relatively secure and has been ranked as such, specifically G4, by NatureServe (see Ranks in Definitions section). However, there is little information on the specifics of its historic and current abundance. *Aquilegia chrysantha* appears to be locally common in parts of west-central Colorado although there is little information on its overall abundance and distribution within the southern part of the state. Throughout its range, *A. chrysantha* tends to grow in isolated occurrences, and there are many areas of apparently potential habitat that remain unoccupied (Lott 1979, Strand and Milligan 1996). Chase and Raven (1975) have suggested that the "initial radiation" of the *A. coerulea*-*A. chrysantha* complex occurred in the central and southern Rocky Mountains through northern Mexico when *Aquilegia* populations, adapted to more mesic conditions, became isolated by increasingly dry conditions in the Upper Miocene. These populations appear to have been isolated over geologic time. Strand et al. (1996) analyzed the variation in chloroplast DNA in the yellow-flowered *Aquilegia* in the southwestern United States and concluded that: "No significant relationship between geographic distance and apparent gene flow between population pairs existed. Further, the estimated level of gene flow was entirely compatible with a historical subdivision of *Aquilegia* populations during the late Pleistocene or early Holocene." Isolated populations of plants that self-fertilize typically exhibit significant differences in genetic variation because different alleles are fixed during inbreeding (Crawford 1983, Barrett and Shore 1989). Small populations of *A. chrysantha* var. *rydbergii* may be genetically depauperate as a result of changes in gene frequencies due to inbreeding or founder effects (Menges 1991). However, the value of such small populations may not be sufficiently appreciated. For example, alleles that were absent in larger populations were only found in small populations of an Astragalus species (Karron et al. 1988). In order to conserve genetic variability, in the absence of genetic (DNA) data, it is likely most important to conserve as many populations as possible in as large a geographic area as possible.

The habitat of *Aquilegia chrysantha* is vulnerable to alteration and destruction throughout its range. In New Mexico and Arizona, it is designated a facultative wetland species by the U.S. Fish and Wildlife Service. Similarly, even though it is designated only a facultative species in Colorado, Nevada, and Utah, *A. chrysantha* is only found in moist areas in Colorado and in moist hanging gardens, stream and seep margins, and other moist areas in Utah (Welsh et al. 1993). Across much of its range, these moist habitats are vulnerable to water development projects. Such projects are likely to increase in the future as populations increase and water becomes less available. Water tables in many regions of the western United States have already fallen precipitously. Extirpations of sites are likely to lead to irreversible local extinctions. Strand (1997) reported that seed dispersal is rare between populations. The inference of the research results of Strand and Milligan (1996) was that no unpopulated habitats are being currently colonized, and thus extirpated populations are unlikely to be re-colonized naturally.

It is clear that the occurrences of *Aquilegia chrysantha* in Colorado represent disjunct and isolated populations at the northern edge of its range. In addition, this species occurs in habitat that is vulnerable to destruction and alteration. Therefore, even as a small-flowered variant of *A. chrysantha*, the populations appear worthy of conservation concern. If the consensus of further evaluation and study establishes var. *rydbergii* as a unique taxon, then the management of this taxon becomes even more critical.

Tools and practices

Documented inventory and monitoring activities are needed to clarify the status and vulnerability of *Aquilegia chrysantha* var. *rydbergii*. Most of the occurrence information is derived from herbarium specimens or relatively casual observations by botanists and does not provide quantitative information on the abundance or spatial extent of the populations. The relatively few collections may not accurately reflect the number of sub-occurrences of this taxon (Kelso personal communication 2003). However, the taxon does appear to exist in only a few populations in a limited geographic range and within a restricted (moist) habitat.

Species inventory

Inventory activities are important for *Aquilegia chrysantha* var. *rydbergii*. It appears that there is a possibility that it can be mistaken in the field for pale variants of *A. coerulea* (see Systematics and synonymy section). This potential for mis-identification needs to be considered during field studies. The current field survey forms for endangered, threatened, or sensitive plant species used by the Gunnison National Forest and the Colorado Natural Heritage Program both request the collection of data that are appropriate for inventory purposes. The number of individuals, the area they occupy and the apparent potential habitat are important data for occurrence comparison. The easiest way to describe occurrences over a large area may be to count patches, making note of their extent, and to estimate or count the numbers of individuals within patches. Collecting information on demographic stages (flowering plants versus rosettes versus seedlings) is also valuable in assessing the vigor of an occurrence. Observations on habitat are also an integral part of a comprehensive species inventory.

Habitat inventory

The available information on habitat supplied with descriptions of occurrences is generally in insufficient detail to make accurate analyses. These habitat descriptions suggest that, within the restrictions of the eco-climate zones in which it exists, this taxon grows in a variety of moist habitats. There is an insufficient understanding of all the features that constitute potential habitat to be able to make a rigorous inventory of areas that will actually be colonized (see Conservation of the Species in Region 2 section). There also have been no studies that relate the abundance or vigor of populations to habitat conditions.

Population monitoring

No monitoring or demographic studies have been reported. Permanent transects may be the most accurate way to study long-term trends of *Aquilegia chrysantha* var. *rydbergii*. Lesica (1987) has discussed a technique for monitoring non-rhizomatous, perennial plant species using permanent belt transects. Elzinga et al. (1998) and Goldsmith (1991) have discussed using a rectangular quadrant frame along transect lines to effectively monitor the "clumped-gradient nature" of populations; that would apply to some populations of *A. chrysantha* var. *rydbergii*. Lesica and Steele (1994) discussed the monitoring implications of prolonged dormancy in vascular plants such as that exhibited by *A. chrysantha*. They concluded that population estimates of plants with prolonged dormancy based on random sampling methods will often underestimate density. They also considered that demographic monitoring studies of species with prolonged dormancy would require longer periods of time to obtain useful information. In order to monitor change in population density with a reduced risk of bias, establishing permanent monitoring plots with repeated measure analysis may be most effective (Lesica and Steele 1994).

It should also be considered that monitoring permanent plots might lead to problems associated with spatial auto-correlation (Goldsmith 1991). If the size of the plot is too small or if the establishment of new plots is not part of the original scheme, when plants die and no replacement occurs within the plot it is impossible to know the significance of the change without studying a very large number of similar plots. Given the likely short-distance of seed dispersal and that adult plants are understood to be long-lived, it is expected that patches of *Aquilegia* plants would be persistent. However, this has not been confirmed. There may be a series of colonizations and local extirpations of patches. Therefore, it is important to monitor the areas between sub-populations because the population dynamics are not known and shifts in stands within a population need to be recognized.

Information on size, or size class, rather than age of the individuals, may be most effectively included in the monitoring scheme (see Demography section). Monitoring protocols typically include a measure of the abundance of noxious weeds. Appropriate action can then be taken in a timely manner.

Habitat monitoring

The relative lack of information on habitat requirements makes it premature to consider that habitat monitoring in the absence of plants can effectively occur. Environmental conditions can be related to changes in abundance over the long-term if descriptions of habitat are recorded during population monitoring activities. Conditions several years prior to the onset of a decrease or an increase in population size may be more important than conditions existing during the year that the change is observed. Notes on current land use designation and evidence of land use activities, for example hiking, biking, or livestock grazing, are important to include with the monitoring data.

Population or habitat management approaches

There have been no systematic monitoring programs for *Aquilegia chrysantha* var. *rydbergii* and no documented attempts of active management practices. Beneficial management practices that have been generally implemented by the USFS include restricting recreational vehicle traffic and routing hikers to designated trails (Olson personal communication 2003). Monitoring populations in areas before and after such management practices have been implemented would be an ideal way to determine the benefits.

Information Needs

Examination of material using a combination of molecular and morphological approaches might resolve the taxonomic status of *Aquilegia chrysantha* var. *rydbergii*. It needs to be confirmed whether populations of *A. chrysantha* var. *rydbergii* are unremarkable small-flowered variants of *A. chrysantha*, or whether the combination of morphological features listed by Rydberg (1906) represents significant genetic diversity (see sub-sections within Classification and description section). Determining the genetic uniqueness of var. *rydbergii* also is necessary for assessing the applicability of studies on var. *chrysantha* (for example those in New Mexico) to management. More comprehensive information on the distribution, abundance, and vulnerability of *A. chrysantha* may be appropriate. Considering its habitat, it would appear to be most vulnerable to both anthropomorphic activities and to global climate change in the drier parts of its range. However, this is speculation that also needs to be evaluated by further survey.

There is little information on population structure and persistence of either individuals or populations of *Aquilegia chrysantha* var. *rydbergii*. Periodic monitoring of existing sites and inventory would clarify the situation. Monitoring pre-existing sites is essential in order to understand the implications of existing and new management practices. The impact of a change in management practice can be more accurately assessed if an inventory to collect baseline data is undertaken prior to the change and then periodic monitoring is conducted after the new policy is initiated. Creating a comprehensive inventory of this taxon will aid in evaluating its vulnerability to local extirpations. The Rampart Range, French Creek, and the Rock Creek Canyon area, all in the Pike National Forest, are appropriate areas to survey for additional populations.

The factors that limit population size and abundance and that contribute to the variable occurrence sizes are not known and need to be determined. Habitat requirements, including any association with non-vascular species, need to be more rigorously defined. More information is needed on the life history and population dynamics of this taxon. The rate of colonization and availability of appropriate habitat influences how populations recover after significant disturbance. Considering the potential vulnerability to genetic loss, research needs to be carried out before artificially establishing new populations or including this taxon in vegetation restoration efforts.

The potential impact of non-native invasive species is also unknown. More information on how this taxon responds to increased competition and alien species is important because invasive non-native species are a substantial problem in many regions of Colorado.

The main information needs for *Aquilegia chrysantha* var. *rydbergii* can be summarized:

- ❖ Determine the genetic uniqueness of the taxon;
- ❖ Conduct inventory;
- ❖ Monitor known occurrences;
- ❖ Determine the impact of human activities on populations, in order to promote proactive steps towards threat mitigation;
- ❖ Rigorously define its habitat requirements;
- ❖ Clarify reproductive biology and population dynamics;
- ❖ Evaluate the abundance and vulnerability of the taxon throughout its range.

DEFINITIONS

Allele — Form of a given gene (Allaby 1992).

Allelopathy — The release into the environment by an organism of a chemical substance that acts as a germination or growth inhibitor of another organism (Allaby 1992).

Autogamous or Autogamy — Self-fertilized, self-fertilization.

Caudex — The perennial region between the base of the stem and the top of the roots that is slowly elongating and commonly branched.

Fragmentation of habitat — Continuous stretches of habitat become divided into separate fragments by land use practices such as agriculture, housing development, logging, and resource extraction. Eventually, the separate fragments tend to become very small islands isolated from each other by areas that cannot support the original plant and animal communities.

Geophyte — A land plant that survives an unfavorable period by means of an underground storage-organ (Raunkiaer 1934, Allaby 1992).

Geitonogamy — Fertilization of flowers by pollen from other flowers on the same plant.

Heterozygote — A diploid or polyploid individual that has different alleles at least one locus.

Holocene — An epoch of the Quaternary period, from the end of the Pleistocene to the present time (Bates and Jackson 1984).

Homozygote — An individual having the same allels at one or more loci.

Iteroparous — Experiencing several reproductive periods, usually one each year for a number of years, before it dies.

Loci — Plural of locus. A specific place on a chromosome where a gene is located (Allaby 1992).

Metapopulation — A composite population. That is, a population of populations in discrete patches that are linked by migration and extinction.

Miocene — An epoch of the early Tertiary period – 23.8 to 5.3 million years ago (USDI USGS undated).

Pleistocene — Also referred to as the Ice Age. An epoch of the Quaternary period, beginning two to three million years ago and lasted until the beginning of the Holocene 8,000 years ago (Bates and Jackson 1984).

Polymorphic (polymorphism) — Having several different forms.

Protandrous — The anthers (male organs) mature before the carpels (female organs).

Ranks — NatureServe and the Heritage Programs Ranking system (NatureServe 2003).

> **G4** indicates that *Aquilegia chrysantha* is – "**Apparently Secure**—Uncommon but not rare (although it may be rare in parts of its range, particularly on the periphery), and usually widespread. Apparently not vulnerable in most of its range, but possibly cause for long-term concern. Typically more than 100 occurrences and more than 10,000 individuals."
>
> **T1** indicates that the variety *rydbergii* is – "**Critically Imperiled**—Critically imperiled globally because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction. Typically 5 or fewer occurrences or very few remaining individuals (<1,000) or acres (<2,000) or linear miles (<10)."
>
> **Q used after the T-rank** because the taxon has "**Questionable taxonomy that may reduce conservation priority**—Distinctiveness of this entity as a taxon at the current level is questionable; resolution of this uncertainty may result in change from a species to a subspecies or hybrid, or inclusion of this taxon in another taxon, with the resulting taxon having a lower-priority (numerically higher) conservation status rank. Internet site: http://www.natureserve.org/explorer/granks.htm.

Semelparous — (semelparity) Reproducing once and then dying.

Stochasticity — Randomness, arising from chance. Frankel et al. (1995) replaced the word "stochasticity" by "uncertainty" to describe random variation in different elements of population viability.

Triternate — Three times ternate where ternate is "arranged in three's." That is, ternate with the three main divisions once and once-again ternate (Harrington and Durrell 1986).

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