

**Demographic Monitoring of *Astragalus scaphoides*
at Two Sites in Montana and Idaho**

Final Report

Prepared for

USDI Bureau of Land Management
Butte District Office

Prepared by

Peter Lesica
Montana Natural Heritage Program
State Library Building
1515 East Sixth Avenue
Helena, Montana 59620

January, 1994

© 1994 Montana Natural Heritage Program

This document is to be cited as follows:

Lesica, P. 1994. Demographic monitoring of Astragalus scaphoides at two sites in Montana and Idaho. Unpublished report to UDSI Bureau of Land Management, Butte District. Montana Natural Heritage Program, Helena. 34 pp.

SUMMARY

I conducted a demographic study of Astragalus scaphoides, a regional endemic, at one site in southwest Montana and one in adjacent Lemhi County, Idaho. Individual plants were mapped in permanent plots and followed from 1986 through 1993. I used matrix projection models and elasticity analyses to elucidate important life history parameters and the importance of predation, especially livestock grazing, on population growth.

Astragalus scaphoides is a long-lived perennial. Growth and survival of non-reproductive plants is consistently important to population growth, while recruitment and survival of reproductives are important in some years but not others. These results along with the fact that the grazed A. scaphoides population became larger during my study suggest that predation of inflorescences by livestock will have only a small negative effect if it is not consistent. Rotation livestock grazing systems should be compatible with long-term persistence of this species in rangelands.

INTRODUCTION

Passage of the Federal Endangered Species Act of 1973 and subsequent recognition of the value of conserving biotic diversity (Wilson 1988) have resulted in many government agencies becoming active in species conservation. Surveys to determine the location and size of populations of rare species are being conducted on public lands throughout the west. These surveys are necessary in any species conservation program; however, knowing the location and size of populations at any one point in time is only the first step in a long-term protection strategy (Sutter 1986). Extinction is a process requiring an understanding of population dynamics (Menges 1986). Periodic inventories can detect trends but will do little to determine causality or help generate predictive hypotheses (Palmer 1987). Long-term conservation requires a knowledge of many life history parameters including fecundity, recruitment, survivorship, age structure, and population flux. Demographic monitoring techniques can provide information on factors regulating population density and persistence (Palmer 1987). This information, in turn, provides an essential basis for management decisions.

Astragalus scaphoides (Jones) Rydb. (Bitterroot milkvetch) is endemic to a small area of east-central Idaho and adjacent Beaverhead County, Montana. It was a candidate for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service but has recently been downlisted to 3C (USDI-FWS 1993). Astragalus scaphoides is listed as sensitive in Idaho (Moseley and Groves 1990) and Montana (Lesica and Shelly 1991). Most populations of A. scaphoides in Montana are on public lands

administered by the Bureau of Land Management and are subject to livestock grazing (Lesica and Elliott 1987a).

Previous studies have indicated that inflorescence predation and seed predation by insects may be adversely affecting A. scaphoides fecundity (Lesica and Elliott 1987a, 1989). Lowered fecundity is thought to be the cause of local rarity in a number of plant species (Greig-Smith and Sagar 1981, Hester and Mendelssohn 1987, Cabin et al. 1991). Here I report the results of an eight-year demographic monitoring study of A. scaphoides at two sites. I use stage-based transition matrix models and elasticity analysis (Caswell 1989, de Kroon et al. 1986) to examine population stability and predict the effects predation, especially livestock grazing on this rare species.

METHODS

Study Sites

The Sheep Corral Gulch population occurs in southern Beaverhead County, Montana on a gentle south-facing slope at 6,300 ft (T8S R12W S16). Mean July and January temperatures at Dillon, 20 miles to the northwest at 5,400 ft, are 66.2° and 20.1°F respectively. Mean annual precipitation is 9.5 in. Vegetation is dominated by Artemisia tridentata and Agropyron spicatum. Aster scopulorum and Phlox hoodii are common forbs. Evidence of heavy spring grazing by livestock was observed in 1989, 1990 and 1993.

The Haynes Creek population is in central Lemhi County, Idaho, approximately 30 miles west of Sheep Corral Gulch. It occurs on a moderate southeast-facing slope at 5,100 ft (T19N R23E S2). Mean July and January temperatures at Salmon, 15 miles northwest at 3,900 ft, are 61.3° and 19.8°F respectively. Mean annual precipitation is 9.93 in. Vegetation is dominated by Artemisia tridentata, Agropyron spicatum and Bromus tectorum. This site was not grazed by livestock before early July during the course of my study.

Field Methods

Two permanent monitoring transects were established at each of the study sites in early July, 1986 following methods outlined in Lesica (1987). Transects were located subjectively to represent the populations. At each site the transects were parallel to each other and the slope and separated by ca. 30 ft. Procedures for reading the monitoring transects are outlined in Lesica and Elliott (1987a) and Lesica (1987). Each transect consisted of 50 1-m² quadrats placed along the transect line. The position of each A. scaphoides plant encountered in the quadrats was mapped and classified for three traits: size,

inflorescence production, and fecundity. The classification system and codes for these traits are as follows:

1) Size Classes:

- D Dormant (no above-ground parts observed)
- S Small non-reproductives (1-3 leaves)
- L Large non-reproductives (≥ 4 leaves)
- R Reproductive

Reproductive plants were classified by the fate of the individual inflorescences as follows:

2) Inflorescence Production:

- A An inflorescence that produced no fruit
- P An inflorescence that was removed by predation
- I An inflorescence that produced at least one mature fruit

3) Fecundity: the total number of mature fruit

Plants that produced inflorescences were classified by using combinations of the classifiers followed by numerics. For example, a reproductive plant with 2 aborted inflorescences, 1 predated inflorescence, and 3 fruit-bearing inflorescences with 10 fruits would be recorded as A2-P1-I3-F10. A complete record of all plants recorded during the study is given in Appendix A. For the purpose of analysis "J" and "M" classes during the study were combined to form the "large non-reproductive" class. Transects were read on July 1-7, 1986-93.

I found that some plants would go undetected for one to several years but reappear in subsequent years. These "dormant" plants may have produced small leaves that had senesced and disappeared by early July; however, my observations in May and June suggest that most of them produced no vegetation on the years in question. The presence of dormant plants can be inferred by comparing transect maps from the full sequence of years. The proportion of dormant plants ranged from 1-23% with a mean of 10% in 1987-91. Plants have "disappeared" for as many as five years before reappearing. However, in 1986-92 at the two sites, 71% of the dormant plants reappeared after one year, and 88% reappeared after two years. As a result, ca. 10% of the plants were undetected in the first and last of years of the study, 3% were undetected in second and second from last years, and ca. 1% were undetected on other years. Thus, I have chosen to eliminate the first and last years (1986, 1993) of the study from demographic analysis.

On years when fruit production was adequate, I collected 50 randomly selected mature fruits from at least 25 plants. I opened the pods, counted the intact seeds, and recorded whether

the fruit contained evidence of insect predation. Weevil larvae (Family Curculionidae) have been observed in the fruits of Astragalus scaphoides (Lesica and Elliott 1987a)

Data Analysis

Stage-structured transition matrix projection models summarize the way in which survival, growth and reproduction at various life-history stages interact to determine population growth (Caswell 1989, van Groenendael et al. 1988). Matrix projections assume fixed transition probabilities between stages in a population through time (Lefkovitch 1965, Menges 1990). They assume density-independent population growth and thus do not give an accurate projection of long-term population future. Nonetheless, they can be used to summarize short-term population dynamics or compare the dynamics of two populations (Caswell 1989). One-year transition probabilities were estimated as the number of plants in life-stage class i moving into class j over the course of one year divided by the number of plants in stage i at the beginning of the year. This method assumes that an individual's transition depends only on its life-stage class at the beginning of the period and is independent of its transition the previous year. The equilibrium growth rate (λ) is the dominant eigenvalue of the transition matrix (Caswell 1989, Lefkovitch 1965). $\lambda > 1.0$ indicates population increase, while $\lambda < 1.0$ indicates decrease. λ integrates the effects of survival, growth and fecundity of the different life-history stages into a single parameter. Details on the construction and use of matrix population models can be found in Caswell (1989) and Menges (1990).

Elasticity measures the relative change in the value of λ in response to changes in the value of a transition matrix element. Elasticity matrices allow comparison of relative importance to population growth and fitness among the various life history transitions (de Kroon et al. 1986). Elasticities sum to unity and regions of the matrix may be summed to compare the importance of growth and survival to recruitment (Caswell 1989). Elasticities for non-reproductive plants are sums from the small (S) and large (L) classes.

When the majority of seeds pass directly from production to germination in less than one year, seeds should not appear as a separate stage in matrix models (Caswell 1989, Silvertown et al. 1993). Seeds of Astragalus scaphoides germinate readily without stratification (Lesica and Elliott 1987b), suggesting that most seeds germinate the same year they are produced. Nonetheless, A. scaphoides may form a seed bank. Not including a seed bank in the matrix model may effect the value of λ (Kalisz and McPeck 1992), especially when it is lower than 1.0. However, it will have little effect on the analyses based on elasticities. I calculated separate elasticities for reproductive transitions and

recruitment by dividing the reproductive+recruitment elasticities proportionately between the two components.

I surveyed a large Astragalus scaphoides population at Hayden Creek, Idaho in late May, 1990 for inflorescence predators. Insects observed girdling stems were collected and sent to the Montana State Entomology Lab in Bozeman for identification.

RESULTS

Population Growth

The number of Astragalus scaphoides plants in the transects at both sites increased by about one third between 1986 and 1993 (Fig. 1). Equilibrium population growth rate (λ) was near or above 1.0 at both sites over the course of the study and was greater than 2.5 at Sheep Corral Gulch in 1988-89 and 1990-91. At no time during the study was λ less than 0.8 at either site (Fig. 2, Appendix B).

Survivorship

Nearly 50% of the plants observed at the start of the study in 1986 were still alive in 1993 (Fig. 3). The first large bout of recruitment during my study occurred in 1989 at Sheep Corral Gulch and in 1988 at Haynes Creek. Survivorship curves for these cohorts are shown in Fig. 3. Fifty percent of Astragalus scaphoides plants survived for more than 3-4 years. Taken together these results suggest that A. scaphoides is a long-lived perennial, with 50% mortality occurring in the first 3-4 years, but a large proportion of plants living to be ten years or older.

Reproduction and Predation

Reproduction varied greatly among years at the two sites (Fig. 5). At Sheep Corral Gulch, the proportion of reproductives was less than 5% in four out of eight years, while at Haynes Creek at least 10% of the population was reproductive in all but one year. The proportion of reproductive plants was higher at Haynes Creek in all eight years of the study.

Predation of whole inflorescences was typical at both sites and can have two possible sources: (1) livestock or (2) insects. Livestock predation was observed only at Sheep Corral Gulch in 1989, 1990 and 1993. Ants (Subfamily Formicinae) and moth larvae (Melacosoma spp., Family Lasiocampidae) were observed removing inflorescences at a site near Haynes Creek in Idaho, and similar damage was observed at both study sites. I did not distinguish between these two sources of inflorescence predation.

Figure 1. Density of Astragalus scaphoides plants at the two study sites in 1987-92.

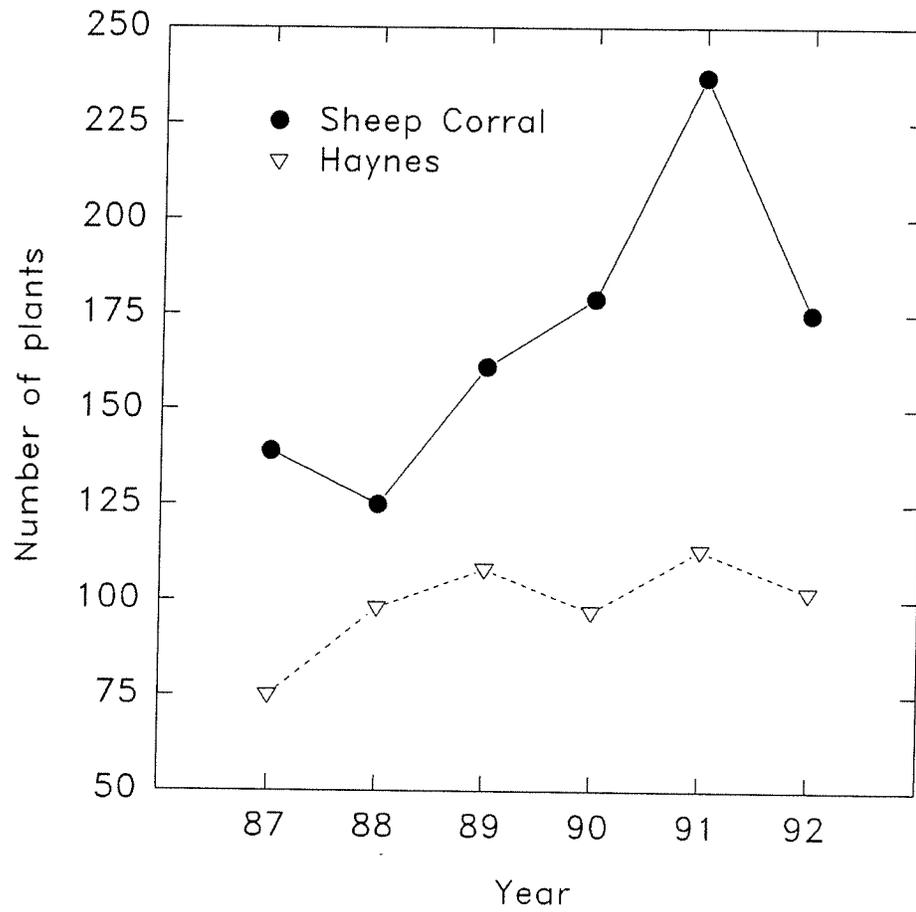


Figure 2. Equilibrium population growth rate (λ) for Astragalus scaphoides sample populations at the two study sites in 1987-92. The "88" value is for 1987-88 etc.

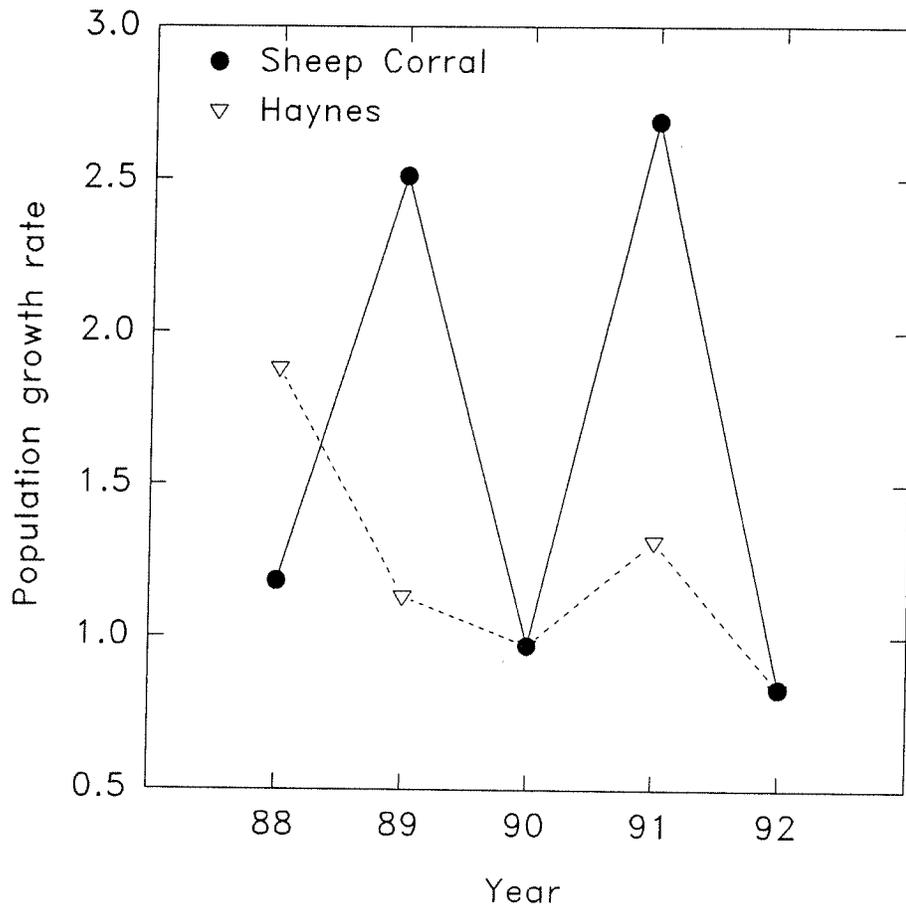


Figure 3. Depletion curves for the 1986 sample population of Astragalus scaphoides at the two study sites:

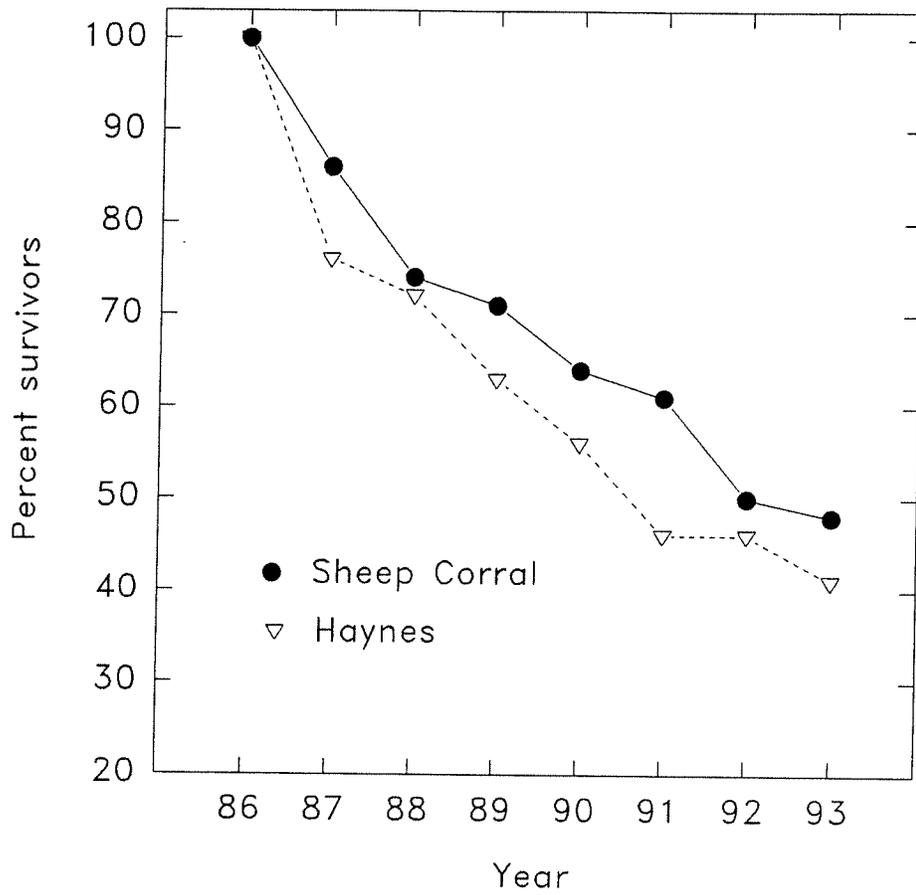


Figure 4. Survivorship curves for the 1989 Sheep Corral Gulch cohort and the 1988 Haynes Creek cohort.

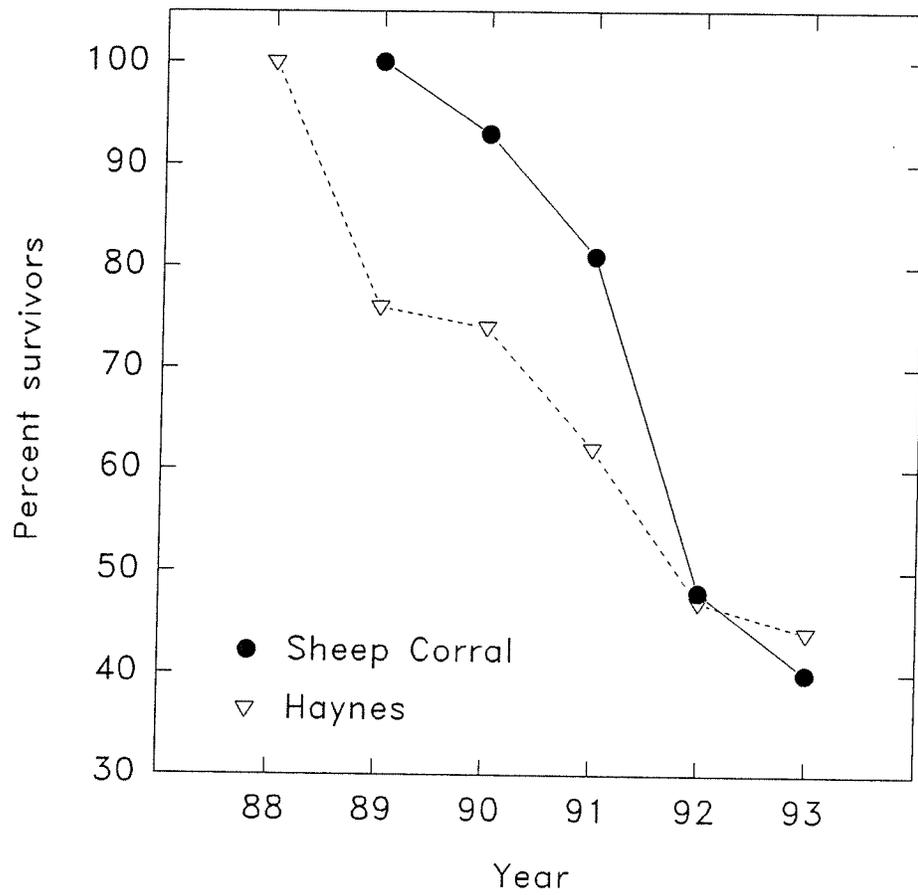
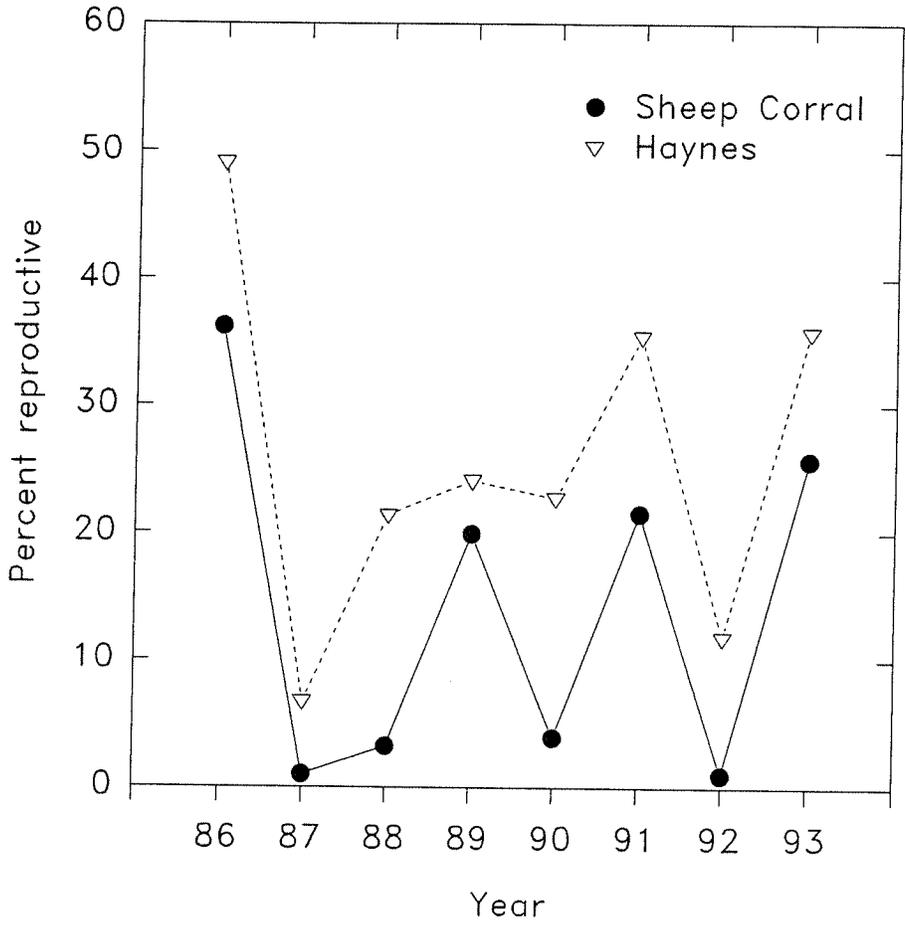


Figure 5. Proportion (%) of reproductive plants in the Astragalus scaphoides sample populations at the two study sites.



The level of inflorescence predation was fairly constant at Haynes Creek over the course of the study, and a significant number of fecund inflorescences were produced in five of eight years (Fig. 6). At Sheep Corral Gulch there was evidence of predation in years with and without evidence of livestock grazing; however, predation was greater in years when livestock were present. In 1993, 85% of the inflorescences were lost to predation, and most of this predation was due to livestock (P. Lesica, personal observation).

Seed predation occurred at both sites in nearly every year in which significant fruiting occurred (Table 1). Overall, loss of seeds to weevil predation ranged from 0-33% with a mean of 18%. Insect seed predation was generally higher at Sheep Corral Gulch than at Haynes Creek (Table 1).

Table 1. Percent loss of seeds to insect seed predators at two study sites. Sample sizes are given in parentheses.

	1986	1988	1989	1990	1991	1993
Sheep Corral	24% (50)	--	33% (50)	--	0% (31)	28% (32)
Haynes Creek	2% (50)	22% (50)	14% (27)	24% (50)	8% (50)	21% (50)

The combined effects of inflorescence and seed predation on fecundity can be severe. In 1988 at Haynes Creek predation reduced fecundity by 62%, while at Sheep Corral Gulch in 1993 fecundity was reduced by 90%.

Elasticity

Elasticity gives the proportional importance of demographic transitions to population growth. Elasticities for five years of transitions for the two study sites are given in Appendix C. Columns of elasticities can be summed to give overall elasticities for life history parameters (Silvertown et al. 1993) Summary elasticities are shown in Fig. 7. Growth and survival of non-reproductives was consistently important at both sites. Survival of dormant plants was very important in two years at Sheep Corral Gulch and one year at Haynes Creek. Survival of reproductives and recruitment were important in about half of the years.

Figure 6. Number of inflorescences that were aborted, predated or that bore fruit in sample populations of Astragalus scaphoides at the two study sites.

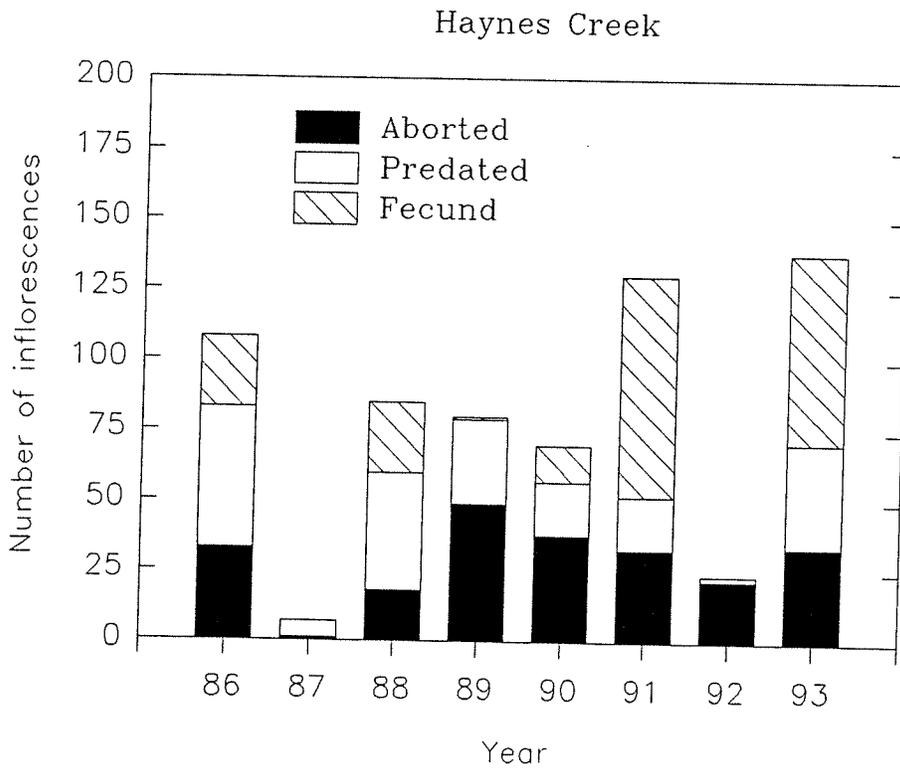
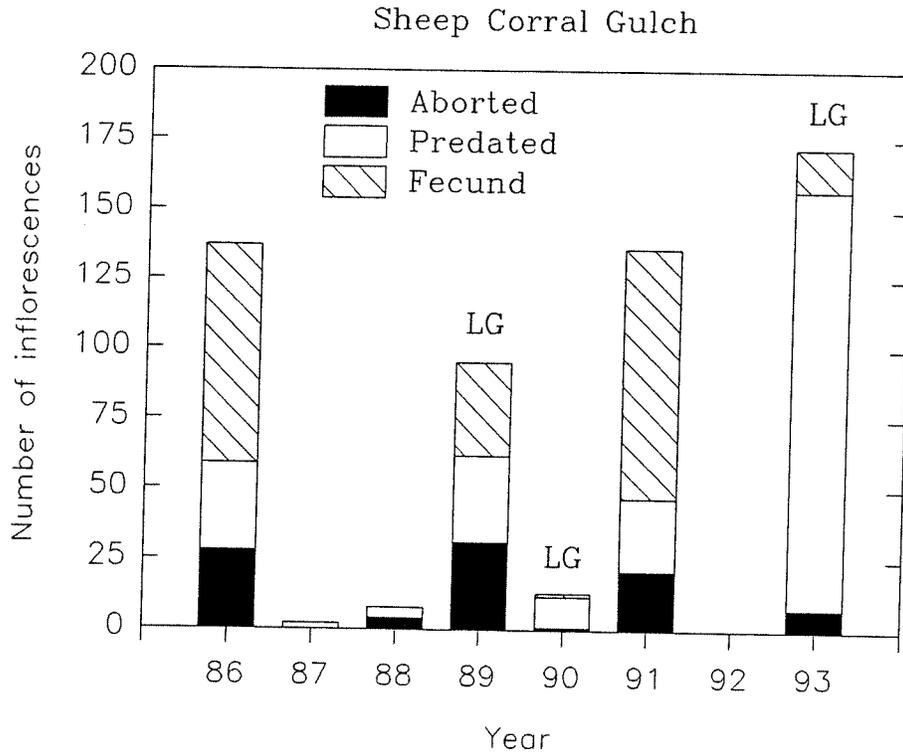
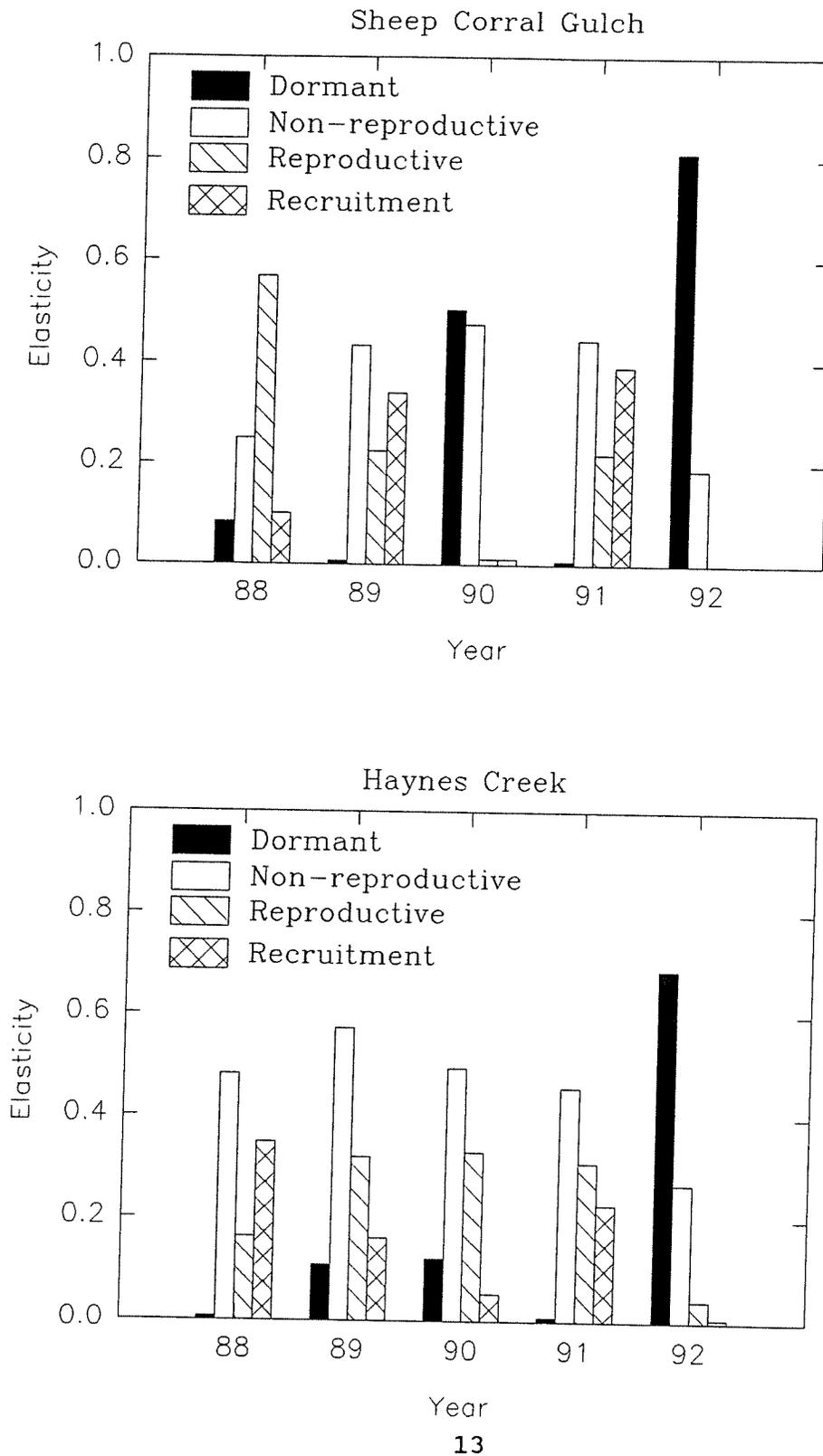


Figure 7. Elasticity values (Appendix C) summed into four life history parameters for *Astragalus scaphoides* sample populations at two study sites in 1987-92: (1) dormant growth and survival, (2) non-reproductive growth and survival, (3) reproductive growth and survival and (4) recruitment.



DISCUSSION

Astragalus scaphoides is a long-lived perennial. Mortality of seeds, seedlings and juveniles is high, but the majority of plants that attain four years of age can probably expect to live for at least ten years and perhaps much longer. The elasticity analysis shows that growth and survival of the non-reproductive plants is the most consistently important life history parameter contributing to population growth and stability. Recruitment from seed was important in less than half the years, and was not of overriding importance in any year. Greater importance for growth and survival has been observed for many long-lived perennial species (Silvertown et al. 1993).

Significant predation of Astragalus scaphoides inflorescences and/or seeds occurred in every year when flowering was at all abundant. However, this predation affected mainly seed production and recruitment and probably had little effect on growth and survival of plants. Since recruitment is only important to population growth in some years and never accounted for more than 40% of λ , inflorescence and seed predation should not have a critical impact on A. scaphoides populations. Even heavy predation should be significant only if it is consistent. These theoretical predictions are supported by the fact that predation was common during the course of the study and was severe in some years, and yet both sample populations expanded.

Livestock are attracted to concentrations of flowering Astragalus scaphoides in the spring and can severely suppress reproduction. At Sheep Corral Gulch, appreciable predation of inflorescences by livestock occurred in 1993 and to some extent in 1989. In 1986 and 1991 A. scaphoides flowered heavily, but livestock were not present in the spring due to a rotation grazing system. It would appear that livestock grazing will not adversely affect A. scaphoides populations unless it is consistent and long-term. Consequently rotation grazing systems should be employed where populations of this rare plant occur.

ACKNOWLEDGEMENTS

I am grateful to Joe Elliott and Lou Hagener for help in the field.

LITERATURE CITED

- Cabin, R. J., J. Ramstetter and R. E. Engel. 1991. Reproductive limitations of a locally rare Asclepias. *Rhodora* 93: 1-10.
- Caswell, H. 1989. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Greig-Smith, J and G. R. Sagar. 1981. Biological causes of local rarity in Carlina vulgaris. In H. Synge (ed.) *The biological aspects of rare plant conservation*. John Wiley and Sons, New York.
- van Groenendael, J, M. de Kroon and H. Caswell. 1988. Projection matrices in population biology. *Trends in Ecology and Evolution* 3: 264-269.
- Hester, M. W. and I. A. Mendelssohn. 1987. Seed production and germination response of four Louisiana populations of Uniola paniculata (Gramineae). *American Journal of Botany* 74: 1093-1101.
- Kalisz, S. and M. A. McPeck. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* 73: 1082-1093.
- de Kroon, H., A. Plaiser, J. M. van Groenendael and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427-1431.
- Lefkovich, L. P. 1965. The study of population growth in organisms grouped by stage. *Biometrics* 21: 1-18.
- Lesica, P. 1987. A technique for monitoring non-rhizomatous, perennial plant species in permanent belt transects. *Natural Areas Journal* 7: 65-68.
- Lesica, P. and J. C. Elliott. 1987a. Distribution, age structure, and predation of Bitterroot milkvetch populations in Lemhi County, Idaho. Report submitted to the Bureau of Land Management, Boise, Idaho.
- Lesica, P. and J. C. Elliott. 1987b. 1987 monitoring study of Bitterroot milkvetch populations in Lemhi County, Idaho. Report submitted to the Bureau of Land Management, Boise, Idaho.
- Lesica, P. and J. C. Elliott. 1989. 1988 monitoring study of Bitterroot milkvetch populations in Lemhi County, Idaho. Report submitted to the Bureau of Land Management, Boise, Idaho.
- Lesica, P. and J. S. Shelly. 1991. Sensitive, threatened and endangered vascular plants of Montana. *Montana Natural Heritage Program Occasional Publication No. 1*, Helena.
- Menges, E. S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. *Natural Areas Journal* 6: 13-25.
- Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* 4: 52-62.
- Moseley, R. and C. Groves. 1990. Rare, threatened and endangered plants and animals of Idaho. *Idaho Natural Heritage Program*, Boise.
- Palmer, M. E. 1987. A critical look at rare plant monitoring in the United States. *Biological Conservation* 39: 113-127.

Silvertown, J., M. Franco, I. Pisanty and A. Mendoza. 1993. Comparative plant demography - relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465-476.

Sutter, R. D. 1986. Monitoring rare plant species and natural areas - ensuring the protection of our investment. *Natural Areas Journal* 6: 3-5.

USDI-Fish and Wildlife Service (1993) Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species; notice of review. *Federal Register*, 58, 51144-51190.

Wilson, E. O. 1988. *Biodiversity*. National Academy Press, Washington D.C.

Appendix A. Life history/size stages for *Astragalus scaphoides* plants in monitoring transects at two study sites in 1986-93. Stage classes are described in Methods section.

		Sheep Corral Lower							
		1986	1987	1988	1989	1990	1991	1992	1993
2a	--	--	--	--	--	--	M	--	--
b	--	--	--	--	--	--	J	--	--
c	--	--	--	--	--	--	S	--	--
3a	S	D	D	S	S	S	M	--	--
b	--	--	--	--	--	--	J	--	--
c	--	--	--	--	--	--	S	--	--
4a	--	--	--	S	S	S	--	--	--
b	--	--	--	--	S	S	S	D	S
5a	A1-P1-12-F15	M	M	M	P4	M	A1-11-F6	D	P8
b	A1-15-F52	M	M	M	P4	S	M	D	P4
c	--	M	D	D	D	D	D	D	S
d	--	--	--	--	S	--	--	--	--
e	--	--	--	--	--	--	--	--	S
f	--	--	--	--	--	--	--	--	S
6a	S	M	J	J	J	J	M	D	I2-F2
b	I1-F7	M	D	M	D	D	J	D	J
c	J	S	D	P2	M	M	A1-11-F8	S	A1-P1
d	--	M	--	--	--	--	--	--	--
e	--	--	--	S	--	--	--	--	--
f	--	--	--	--	--	--	--	--	J
g	--	--	--	--	--	--	J	S	S
7a	S	--	--	--	--	--	--	--	--
8a	S	S	S	J	S	S	M	D	J
b	P1-11-F11	M	S	A1-11-F2	J	M	M	D	PHB
c	J	M	S	J	--	--	--	--	--
d	--	--	--	--	--	--	J	--	--
9a	--	--	--	--	--	--	S	S	S
b	--	--	--	--	--	--	S	S	S
10a	--	--	--	--	--	--	S	--	--
b	--	--	--	--	--	--	--	S	S
11a	P1-11-F11	M	--	--	--	--	--	--	--
b	I2-F10	M	D	D	D	D	S	--	--
c	S	S	--	--	--	--	--	--	--
d	--	--	--	--	--	--	S	--	--
e	--	--	--	--	--	--	S	D	S
f	--	--	--	--	--	--	S	--	--
12a	S	--	--	--	--	--	--	--	--
b	--	--	--	--	--	--	J	D	J
c	--	--	--	--	--	--	S	--	--
d	--	--	--	--	--	--	S	--	--
e	--	--	--	--	--	--	S	S	J
13a	--	S	--	--	--	--	--	--	--
b	--	M	S	--	--	--	--	--	--
c	--	--	--	--	--	--	--	--	--
d	--	--	--	S	--	--	--	--	--
e	--	--	--	--	S	--	--	--	--
f	--	--	--	--	--	S	S	D	S
g	--	--	--	--	--	--	S	S	S
h	--	--	--	--	--	--	--	S	J
i	--	--	--	--	--	--	--	--	S
14a	J	S	S	S	S	S	J	D	P2
b	S	D	D	D	D	D	S	S	--
c	S	D	D	D	D	D	S	--	--
15a	S	--	--	--	--	--	--	--	--
b	J	M	--	--	--	--	--	--	--
c	--	M	D	M	--	--	--	--	--
d	--	--	S	D	M	M	M	S	M
e	--	--	--	--	S	S	D	D	S
16a	S	--	--	--	--	--	--	--	--
b	J	M	M	J	J	J	I2-F5	D	S
c	--	M	D	M	J	J	I2-F10	S	P2
d	--	--	--	--	--	S	--	--	--

e	f	g	h	i	j	34a	b	c	d	e	35a	b	36a	b	c	d	e	37a	b	c	d	38a	b	c	d	e	f	g	39a	b	40a	b	41a	42a	b	c	43a	b	c	d	e	f				
---	---	S	J	S	P1	---	---	---	---	---	J	---	I2-F10	---	---	---	---	S	---	---	---	---	---	---	---	---	---	---	---	J	---	---	J	---	---	---	---	A1-I1-F3	S	---	---	---	---			
M	---	M	M	M	M	S	---	---	---	M	---	---	---	---	---	---	M	---	---	---	---	---	---	---	---	---	---	---	M	---	---	---	---	M	---	---	M	---	M	---	M	S	---	---	---	---
D	---	M	D	P2	S	---	---	---	---	S	---	---	---	---	---	S	---	---	---	---	---	---	---	---	---	---	---	---	M	---	---	---	---	S	D	---	S	S	---	S	---	---	---	---		
A1-I1-F4	---	S	D	P2	J	M	---	---	---	J	---	---	---	---	---	P2	S	---	---	---	S	---	S	S	---	---	---	S	M	S	---	---	M	---	S	---	J	---	J	---	S	J	---	J		
J	---	J	D	D	S	S	---	---	---	S	S	---	J	S	---	---	---	---	---	S	S	---	D	S	---	---	---	S	S	S	---	S	S	---	D	---	S	---	S	---	S	---	S	S		
S	---	S	I4-F17	M	M	---	---	---	---	J	J	---	A1-I1-F2	S	D	S	S	A1-I2-F16	A1	---	S	S	S	---	D	J	J	S	S	S	---	J	S	I3-F16	S	---	M	---	J	---	I4-F4	---	S	I6-F30		
D	---	D	D	D	---	D	D	---	---	S	D	D	---	S	J	---	S	S	D	D	---	D	---	S	---	J	---	S	---	---	---	---	---	S	S											
J	S	S	---	J	---	S	P6	---	---	M	A1	S	P4	S	S	---	---	P1-I1-F5	P6	---	J	S	S	S	---	S	J	---	J	---	S	S	J	---	---	P2	S	J	---	---	---	J				

b	I1-F5	S	D	A1-11-F5	S	A1	M	P2
c		M			S	D	S	S
d					S	S	S	S
e					S	S	S	S
f					S	S	S	S
g					S	S	S	S
h					S	S	S	S
39a					S	S	S	S
b					S	S	S	S
c					S	S	S	S
d					S	S	S	S
40a		M	D	A1-11-F2	J	I2-F12	S	S
b		M	J	J	M	M	S	S
c				S	S	S	S	S
d				S	S	S	S	S
e					S	S	S	S
41a	A1-113-F44	M						
b								
c								
d								
e								
f								
g								
42a	J							
b		S	S					
c		S	S					
43a								
b								
c								
d								
e								
f								
44a	A2	M	D					
b								
45a	S	M	J					
b								
c								
46a	J	M						
b								
c								
d								
e								
f								
g								
h								
i								
j								
k								
47a	J							
b	A1-15-F25	M	J					

Haynes Lower

	1986	1987	1988	1989	1990	1991	1992	1993
1a	A3-13-F15	A1-F0	P4-1-3-F22	A1-P1-F0	A2-13-F18	A2-P1-16-F56	D	A3-12-F6
b		M	A1-P6-12-F20	A2-P1-F0	A4-F0	A2-13-F27	D	A2-P2
c			S	J	P2-F0	M	D	J
d				J	S	J	J	A1
e						M	J	J
f						S	S	I1-F2
g						S		
h						J		
2a			S	S		J	S	
b						J	S	
c						J	J	A1-P2
3a	A1-P2-13-F15						J	J
b	S							
c	A2-P1-11-F3	M						
d	A4-P1-12-F11	D	S	D	D	D	D	J
e								S
f								S
4a	A4-P2-13-F18	P1-F0						
b	J	D			D	D	D	A1
c	P1-11-F3	P2-F0	P2-11-F12	A1-F0	A2-F0	A2-P1-12-F23	A1-P2-F0	A4-P4-12-F10
d			S	S	S	P1-F0	A2-F0	I2-F10
e								S
5a	A1-P1-12-F15	D	D	D	D	J	M	S
b			S	S	S	I2-F5	S	S
c						S	S	P1-11-F1
d						S	D	
e							S	
f								
22a								
28a				S	J	M	A2-F0	S
29a				S	S	J		P1-11-F1
33a	P6-12-F13	M	J	A1-P3-F0	A1-P1-11-F5	M	A4-F0	
b		D	D	A3-F0	A2-F0	P1-F0	J	P1
c								S
d								S
e								S
f								S
34a	S	S	D	D	S	A1-F0	S	S
b	J	D	S					S
c			S	S	M	I2-F11	J	A1-11-F7
d		S	S	D	D	J	S	J
e								
f								
g								
h								
i								

35a	---	S	S	D	M	I2-F12	J	A2
b	---	S	S	J	M	P1-I1-F3	---	---
c	---	S	S	J	M	P1-I1-F3	A3-F0	A1-P4-I2-F14
d	---	S	S	A1-F0	M	I4-F17	A2-F0	A2-I2-F3
e	A2-P1-F0	J	J	D	S	M	M	A1-I3-F32
36a	---	D	D	D	D	J	M	S
37a	---	P10-F0	A11-P2-I4-F7	---	---	---	---	A1
b	---	A1-P4-I3-F15	A5-F0	---	---	---	---	---
40a	S	---	---	---	---	S	S	S
44a	S	---	---	---	---	S	S	S
b	A1-P2-F0	---	---	J	S	---	---	---
45a	J	---	---	J	P2-F0	---	---	---
b	---	---	---	M	M	---	---	---
c	---	---	---	M	P2-F0	P1-I1-F2	M	---
d	J	---	---	J	M	---	---	---
46a	S	---	---	S	---	---	---	---
b	S	---	---	J	---	---	---	---
c	S	---	---	J	---	---	---	---
d	A2-F0	S	---	J	P2-F0	---	---	---
e	A2-P2-I2-F10	S	---	M	M	---	---	---
f	J	---	---	M	P2-F0	---	---	---
g	S	J	J	M	M	---	---	---
h	S	J	J	J	M	---	---	---
i	S	S	S	J	M	---	---	---
j	---	S	S	S	---	---	---	---
k	---	S	S	S	---	---	---	---
l	---	J	J	S	P2-F0	D	D	S
m	---	S	J	S	J	A1-P3-F0	A2-F0	I2-F5
n	---	S	S	S	J	---	---	---
o	---	---	---	S	P2-F0	---	---	---
p	---	---	---	S	P2-F0	M	M	A2
q	---	---	---	J	J	S	---	---
47a	J	P6-F0	---	---	---	---	---	S
b	---	S	---	A3-P2-F0	---	---	---	---
c	---	---	---	A1-P1-F0	A4-F0	---	---	---
d	---	---	---	S	M	J	---	---
e	---	---	---	---	---	S	---	---
f	---	---	---	---	---	---	---	M
48a	---	---	---	---	---	---	---	S
49a	---	---	---	---	---	---	---	I2-F13
50a	A4-I2-F12	M	P2-12-F9	M	I7-F41	J	J	S
b	---	---	---	---	S	P2-12-F22	S	S
c	---	---	---	---	---	S	S	---
d	---	---	---	---	---	---	S	S
e	---	---	---	---	---	---	S	---
f	---	---	---	---	---	---	S	---
g	---	---	---	---	---	---	S	---
h	---	---	---	---	---	---	S	---
i	---	---	---	---	---	---	S	---
j	---	---	---	---	---	---	S	---

McDevitt Lower

1a	A2-I10-F71	J	P4-F0	J	J	M	---	---	---	J	---	---
b	---	J	S	J	J	---	---	---	---	---	---	---
c	---	M	---	---	---	---	---	---	---	---	---	---
2a	A4-I1-F2	M	A1-P2-F0	M	A1-F0	P1-F0	A1-P1-F0	P1-F0	A2-F0	J	---	---
b	---	P2-F0	---	D	---	S	---	---	---	---	---	---
c	A2-I4-F13	P1-F0	---	D	---	J	---	---	---	---	---	---
3a	---	---	---	---	---	---	---	---	---	---	---	---
b	---	P1-F0	---	---	---	---	---	---	---	---	---	---
5a	---	---	---	---	---	---	---	---	---	---	---	---
11a	---	---	---	---	---	---	---	---	---	---	---	---
13a	A14-P1-I3-F6	---	A15-P1-I17-F58	---	---	---	---	---	---	---	---	---
15a	---	---	---	---	---	---	---	---	---	---	---	---
16a	---	---	---	---	S	---	---	---	---	---	---	---
b	---	---	---	---	S	---	A1-I1-F11	---	---	J	---	---
17a	I1-F3	J	---	D	---	S	---	---	---	J	---	---
b	A4-F0	A3-I3-F3	---	M	---	M	---	---	---	---	P2-F0	---
c	J	S	---	S	---	M	---	---	---	---	---	---
d	A1-F0	M	---	M	---	S	P5-I1-F14	---	---	---	P1-F0	---
e	---	S	---	S	---	S	---	---	---	---	S	---
f	---	---	---	S	---	S	---	---	---	---	S	---
g	---	---	---	S	---	---	---	---	---	---	---	---
h	---	---	---	---	---	---	---	---	---	---	---	---
19a	---	---	---	---	S	---	---	---	---	---	S	---
b	---	---	---	S	---	---	---	---	---	---	S	---
20a	S	---	---	J	---	---	---	---	---	---	---	---
21a	A7-I5-F25	---	---	J	---	J	---	---	---	---	J	---
b	J	A4-P2-I1-F1	---	---	A1-F0	---	P2-I1-F10	---	---	---	---	---
c	J	---	---	---	---	---	---	---	---	---	---	---
d	A4-F0	A3-I1-F9	---	---	---	---	---	---	---	---	---	---
22a	A2-P1-F0	P1-F0	---	---	---	---	---	---	---	---	---	---
b	S	S	---	J	---	D	---	---	---	S	---	---
23a	J	S	---	J	---	I1-F3	---	---	---	J	---	---
b	A5-F0	A5-P1-I4-F20	---	---	---	---	---	---	---	---	---	---
25a	S	J	---	J	---	I2-F9	---	---	---	---	---	---
b	A3-I5-F25	A2-F0	---	M	---	---	---	---	---	S	---	---
c	S	M	---	J	---	---	---	---	---	---	---	---
d	---	S	---	J	---	---	---	---	---	---	---	---
e	---	J	---	S	---	---	---	---	---	---	---	---
f	---	S	---	S	---	---	---	---	---	---	---	---
26a	A5-P4-I3-F20	P8-A2-I3-F11	---	S	---	---	---	---	---	---	---	---
27a	A7-F0	A3-P1-I1-F1	---	J	---	P3-I3-F17	---	---	---	S	---	---
b	A6-P1-I2-F10	M	---	J	---	A1-I2-F11	---	---	---	---	---	---
30a	A3-F0	---	---	---	---	---	---	---	---	---	---	---
32a	A3-I7-F28	M	---	A3-I1-F1	---	P4-I3-F25	---	---	---	J	---	---
34a	I1-F9	A5-I2-F20	---	M	---	P2-I1-F?	---	---	---	---	---	---
b	S	J	---	J	---	---	---	---	---	M	---	---
38a	A1-I1-F2	A4-I2-F4	---	J	---	---	---	---	---	---	---	---
b	A3-I1-F10	I3-F12	---	M	---	I2-F0	---	---	---	---	---	A1-F0

36a	I1-F4	M	--	--	--	--
b	I3-F12	M	M	--	--	--
37a	A1-F0	--	--	--	--	--
b	J	A1-12-F2	J	P4-F0	A2-F0	
c	A5-11-F2	J	D	D	A1-P1-F0	
d	--	A4-P5-F0	S	J	I1-F1	
38a	S	S	--	J	S	
b	--	--	D	I1-F2	M	
39a	--	S	S	P2-F0	--	
b	--	--	--	--	--	
c	--	--	S	S	S	
40a	A1-P1-15-F13	A3-P4-F0	M	P2-F0	--	
41a	P3-F0	A7-P2-16-F29	D	M	S	
44a	S	S	S	S	J	
b	--	S	--	--	--	
45a	J	M	--	--	--	
b	--	M	S	I1-F2	--	
47a	J	A1-P3-F0	S	--	--	
b	A1-F0	A3-P2-F0	M	A1-P1-F0	S	
48a	J	M	D	A1-F0	--	
b	J	M	M	--	--	
49a	J	A3-F0	--	--	--	
b	J	A8-11-F5	--	--	--	

Appendix B. Stage-based transition matrices for *Astragalus scaphoides* at two sites in 1987-92. Four stages are recognized: dormant (D), small non-reproductive (S), large non-reproductive (L) and reproductive (R). The reproductive and recruitment columns must be added together before solving for λ , the dominant eigenvalue (see Methods).

Sheep Corral Gulch

1987-88					1990-91				
To	From				To	From			
	D	S	L	R		D	S	L	R
D	.67	.18	.20	0 + 0	D	.14	.06	0	0 + 0
S	.11	.55	.24	0 + 0	S	.21	.23	.06	0 + 9.86
L	.22	.06	.36	0 + 0	L	.50	.42	.26	.29 + 2.42
R	0	0	.03	1.0 + 0	R	.14	.12	.57	1.0 + .14
	$\lambda=1.18$					$\lambda=2.69$			

1988-89					1991-92				
To	From				To	From			
	D	S	L	R		D	S	L	R
D	.23	.04	.02	0 + 0	D	.70	.24	.21	.25 + 0
S	.17	.27	.05	0 + 4.0	S	.30	.27	.37	.33 + .20
L	.43	.53	.45	0 + 7.0	L	0	0	.14	.22 + 0
R	.17	.08	.43	1.00 + .25	R	0	0	0	0 + 0
	$\lambda=2.51$					$\lambda=0.83$			

1989-90				
To	From			
	D	S	L	R
D	.80	.17	.14	.06 + 0
S	.10	.73	.37	.22 + .91
L	.10	.02	.35	.56 + .03
R	0	.02	.01	.16 + 0
	$\lambda=0.97$			

Haynes Creek

1987-88					1990-91				
To	From				To	From			
	D	S	L	R		D	S	L	R
D	.50	.03	.04	0 + 0	D	.21	.03	0	0 + 0
S	.40	.45	.04	0 + 5	S	.21	.34	.03	0 + .95
L	0	.24	.37	0 + 1.16	L	.50	.31	.21	.18 + .27
R	.10	.06	.52	.60 + .20	R	.07	.19	.66	.64 + 0
	$\lambda=1.88$					$\lambda=1.31$			

1988-89					1991-92				
To	From				To	From			
	D	S	L	R		D	S	L	R
D	.57	.13	.04	0 + 0	D	.75	.03	.06	.05 + 0
S	.14	.42	.24	.05 + 1.10	S	0	.44	.30	.15 + .30
L	.14	.16	.28	.14 + .14	L	.25	.08	.36	.53 + .03
R	.14	.04	.32	.67 + .05	R	0	0	.11	.20 + 0
	$\lambda=1.13$					$\lambda=0.83$			

1989-90				
To	From			
	D	S	L	R
D	.64	.12	.05	0 + 0
S	.27	.38	.14	.04 + .23
L	0	.20	.48	.27 + .04
R	.09	0	.33	.58 + 0
	$\lambda=0.97$			

Appendix C. Elasticities for *Astragalus scaphoides* stage transition matrices at three sites for 1987-92. The left three columns(D, S, L) represent non-reproductive growth and survival. The reproductive (R) column represents growth and survival of reproductives. The recruitment column (Rc) represents recruitment from seed.

Sheep Corral Gulch

1987-88						1990-91					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.048	.022	.015	0	0	D	.001	.005	0	0	0
S	.004	.032	.009	0	.024	S	.001	.018	.002	0	.185
L	.032	.015	.055	0	.077	L	.002	.082	.023	.014	.177
R	0	0	.101	.568	0	R	.003	.099	.215	.204	.029

1988-89						1991-92					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.001	.003	.001	0	0	D	.686	.126	0	0	0
S	.001	.017	.002	0	.139	S	.126	.061	0	0	0
L	.002	.081	.049	0	.143	L	0	0	0	0	0
R	.003	.057	.222	.224	.056	R	0	0	0	0	0

1989-90					
	D	S	L	R	Rc
D	.413	.074	.015	.001	0
S	.048	.292	.037	.002	.011
L	.042	.007	.030	.005	.001
R	0	.017	.002	.004	0

Haynes Creek

1987-88						1990-91					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.002	.003	.002	0	0	D	.001	.005	0	0	0
S	.001	.045	.002	0	.141	S	.001	.058	.004	0	.160
L	0	.082	.058	0	.153	L	.004	.080	.038	.046	.068
R	.003	.059	.231	.164	.055	R	.001	.079	.193	.264	0

1988-89						1991-92					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.055	.048	.006	0	0	D	.620	.020	.041	.006	0
S	.007	.086	.020	.005	.113	S	0	.042	.030	.003	.005
L	.015	.064	.044	.028	.028	L	.068	.018	.082	.021	.001
R	.031	.034	.109	.287	.021	R	0	0	.036	.011	0

1989-90					
	D	S	L	R	Rc
D	.081	.028	.013	0	0
S	.023	.061	.024	.007	.039
L	0	.065	.170	.093	.014
R	.018	0	.134	.230	0