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Effects of Juniper Woodland Expansion on Breeding Birds in Grasslands of Northern Arizona

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INTRODUCTION

Since European settlement, pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) (P-J) woodlands have expanded into large portions of the southwestern United States historically occupied by grassland vegetation (Miller 1921, Leopold 1951, Johnsen 1962, Rogers et al. 1984, Cinnamon 1988). Livestock grazing and fire suppression commonly are cited as causes of woodland expansion (Johnsen 1962, West 1984), but other potential causal factors include climate change, (Jameson 1987), long-term biogeographic patterns (Betancourt 1987, Davis 1987), and tree reestablishment following harvest by aboriginal Americans (Samuels and Betancourt 1982).

Patterns of juniper expansion in southwestern grasslands have received little study. Johnsen (1962) noted that invasions generally occurred in areas that were formerly juniper savannahs or grassland inclusions within P-J woodland. However, in northern Arizona, juniper invasion also appears widespread in areas that once were open grasslands. Most developing woodlands are composed primarily of one-seed juniper (*J. monosperma*) or Utah juniper (*J. osteosperma*). Jameson (1962) described a site north of Flagstaff, Arizona, that had "only a few scattered juniper trees" in 1907. By 1960, there were approximately 148 trees/ha, some of which were up to 3-m tall. The typical pattern of expansion is downslope or outward from rocky uplands, sites where juniper was likely most abundant prior to woodland expansion. At many sites in northern Arizona, woodland establishment seems to have occurred as multiple events, well separated in time. In these situations, distinct woodland successional stages can be found, in which tree size and density decrease as one moves away from upland "source" areas.

There has been considerable debate over the degree to which juniper expansion is a "natural" phenomenon and as to whether or not management actions should be taken to reverse the process. Some resource managers have proposed or implemented "ecosystem restoration" projects intended to restore grassland or savannah conditions (e.g., Goodloe 1995, Loftin et al. 1995). Despite these concerns, effects of woodland expansion on grassland wildlife in the Southwest have received limited study and remain poorly understood.

Because grassland bird species are closely tied to vegetation structure (Rotenberry and Wiens

1980, Wiens and Rotenberry 1981, Cody 1985), woodland expansion can substantially change the composition of breeding bird communities. Studies in other North American grasslands suggest that invasion of woody vegetation is a widespread landscape change with potential adverse impacts to grassland avifauna (Knopf 1994, U.S. Department of the Interior 1997). Invasion of grassland by juniper woodland also creates suitable habitat and foraging opportunities for a variety of potential nest predators that can exert considerable influence on the productivity of grassland passerines (Rotenberry and Wiens 1980, Gryzbowski and Pease 1995).

As a group, grassland-breeding birds have shown steeper, more persistent, and more geographically widespread population declines than any other group of North American birds (Peterjohn and Sauer 1995). Because most grassland-breeding birds do not migrate to wintering areas in Central and South America, population declines are likely linked to processes occurring within North American breeding and wintering habitats (Knopf 1994). In the southwestern U.S., woodland expansion may represent a substantial negative impact to grassland avifauna.

My objective in this study was to determine effects of juniper woodland expansion on breeding birds in grasslands of northern Arizona. I studied breeding bird communities along a successional gradient from open, uninvaded grassland to mid-aged juniper woodland. In this study, I measured the following response variables: (1) breeding bird species composition, (2) abundance of individual bird species, and (3) rates of nest predation.

STUDY AREAS

The study was conducted at 2 sites in northern Arizona, representing the transition zone between Plains and Great Basin grasslands (Brown 1982). Grasslands at both sites were undergoing succession to one-seed juniper woodland and had not received treatments intended to control woody vegetation (e.g., herbicide application, prescribed fire, tree cutting, or mechanical control).

The Chevelon site was located 38 km southeast of Winslow, Arizona (Fig. 1). Elevations ranged from 1,834-1,901 m. Annual precipitation averages 20.4 cm. Soils were derived from limestone and sandstone parent materials. Dominant grass species include blue grama (*Bouteloua gracilis*), ring muhly (*Muhlenbergia torreyana*), and bottlebrush squirreltail (*Sitanion hystrix*). Grass cover and grass height ranged from 28.8%-42.6% and 7.4-10.1 cm, respectively (Table 1).

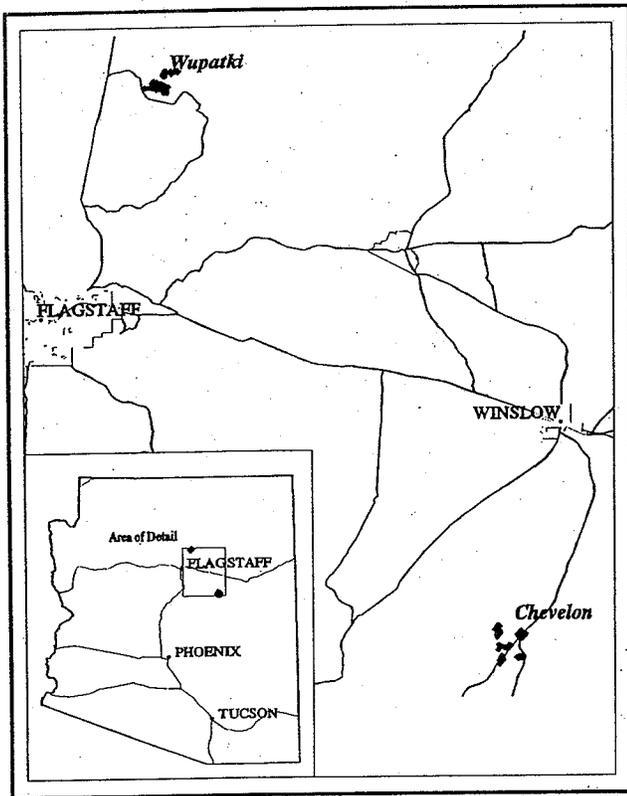


Figure 1. Locations of Chevelon and Wupatki juniper-woodland expansion study sites, 1997-98.

Scattered shrubs were present, primarily four-wing saltbush (*Atriplex canescens*), Bigelow sagebrush (*Artemisia bigelovii*), and Fremont barberry (*Berberis fremontii*). Shrub cover and height ranged from 1.8%-5.2% and 25.7-74.6 cm, respectively (Table 1). Colorado pinyon (*P. edulis*) was present on widely scattered microsites with shallow, rocky soils. The Chevelon site was grazed

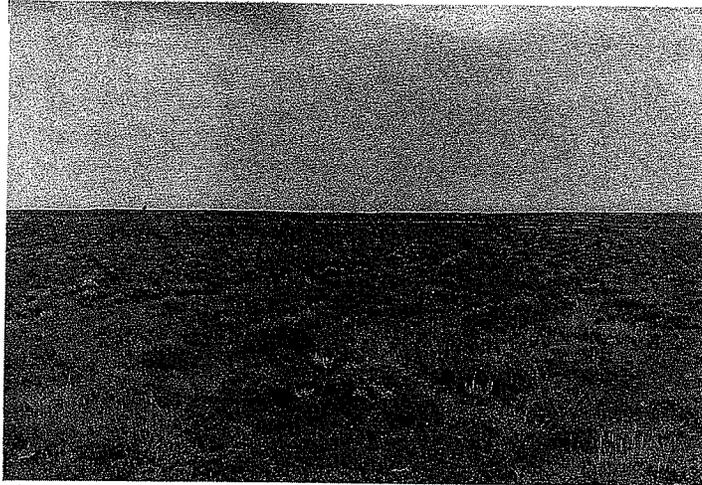
each year by cattle and horses, primarily during winter and spring.

The Wupatki site was located in the north-central portion of Wupatki National Monument, 48 km northeast of Flagstaff, Arizona (Fig. 1). Elevations ranged from 1,591-1,645 m. Annual precipitation averages 20 cm. Soils were derived from limestone and sandstone parent materials and were overlaid by a layer of volcanic cinders. Dominant grass species include needle-and-thread (*Stipa comata*), blue grama, galleta (*Hilaria jamesii*), black grama (*B. eriopoda*), and alkali sacaton (*Sporobolus airoides*). Grass cover and height ranged from 38.9%-57.1% and 25.8-37.2 cm, respectively (Table 1). Shrubs were relatively sparse, consisting largely of rabbitbrush (*Chrysothamnus* spp.). Shrub cover and height ranged from 0.3%-2.1% and 44.5-60.2 cm, respectively (Table 1). Livestock have been excluded from the monument for ca. 20 years.

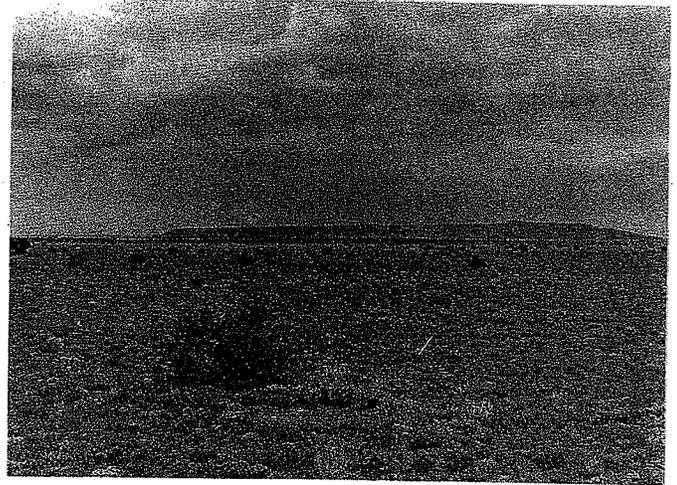
My study areas included 4 successional stages: (1) open, uninvaded grasslands without juniper; (2) grassland undergoing early stages of juniper establishment, with scattered small junipers <25 years old; (3) developing woodland with a higher density of trees that were 50-75 years old; and (4) mid-aged woodland with denser stands of large trees >75 years old. All 4 successional stages were studied at the Chevelon site (Fig. 2). Mid-aged woodland stands at Wupatki were not extensive enough to be included in this study, thus only the first 3 successional stages were included at this site (Fig. 3). Characteristics of successional woodlands at both study sites are summarized in Table 2. Understory vegetation characteristics were very similar across successional stages at both sites (Table 1).

Table 1. Cover and height of grasses and shrubs along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-98. Values are means \pm SE.

Study site	Grass		Shrub	
	Successional stage	Cover (%)	Height (cm)	Cover (%)
Chevelon				
Uninvaded grassland	28.8 \pm 2.9	8.5 \pm 0.4	5.2 \pm 0.4	25.7 \pm 1.5
Early establishment	29.5 \pm 1.8	10.1 \pm 0.3	3.0 \pm 0.3	35.5 \pm 1.1
Developing woodland	30.3 \pm 1.1	7.6 \pm 0.4	2.3 \pm 0.3	49.3 \pm 10.3
Mid-aged woodland	42.6 \pm 1.6	7.4 \pm 0.2	1.8 \pm 0.4	74.6 \pm 9.7
Wupatki				
Uninvaded grassland	57.1 \pm 1.8	35.4 \pm 1.2	0.3 \pm 0.1	60.2 \pm 6.5
Early establishment	54.4 \pm 1.6	37.2 \pm 0.6	1.3 \pm 0.3	53.6 \pm 1.9
Developing woodland	38.9 \pm 2.0	25.8 \pm 0.7	2.1 \pm 0.5	44.5 \pm 1.7



(a)



(b)

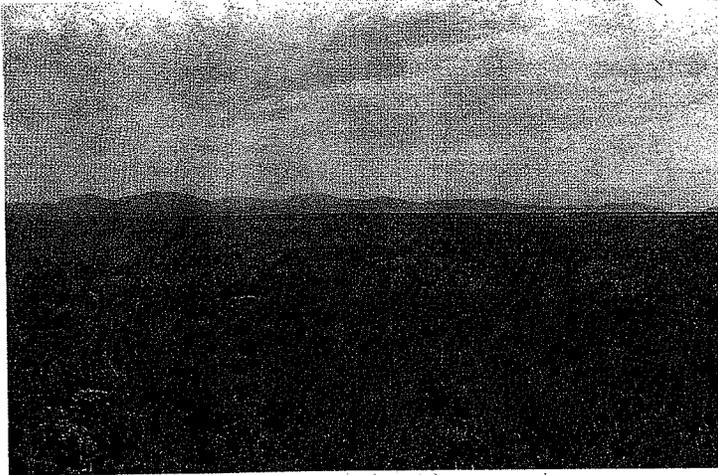


(c)

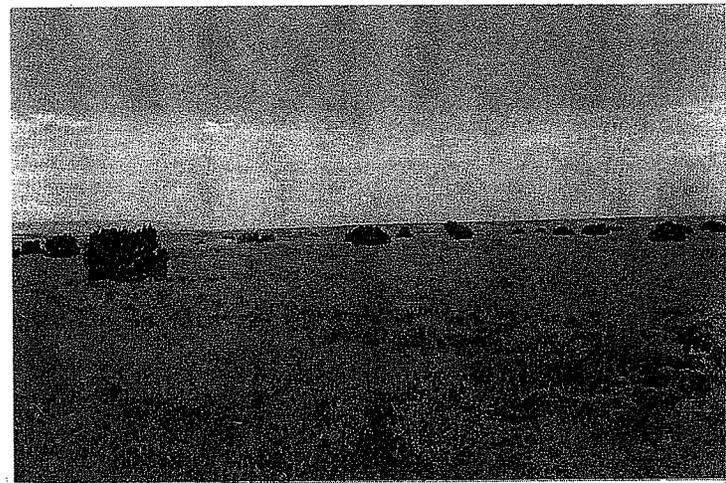


(d)

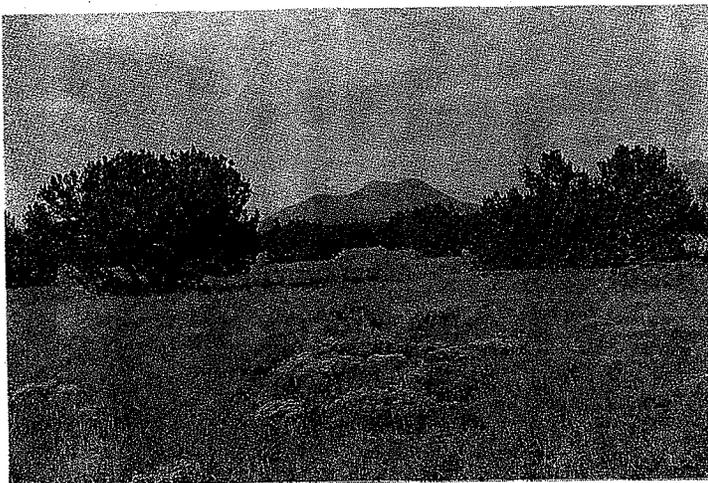
Figure 2. Examples of juniper woodland expansion, Chevelon site: (a) uninvaded grassland, (b) early establishment woodland, (c) developing woodland, and (d) mid-aged woodland.



(a)



(b)



(c)

Figure 3. Examples of juniper woodland expansion, Wupatki site: (a) uninvaded grassland, (b) early establishment woodland, (c) developing woodland.

Table 2. Density and height of one-seed juniper (*Juniperus monosperma*) along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-98. Values are means \pm SE.

Study site			
	Successional stage	Tree density (trees/ha)	Tree height (m)
Chevelon	Uninvaded grassland	0	-
	Early establishment	10.0 \pm 2.5	2.0 \pm 0.2
	Developing woodland	92.3 \pm 8.8	2.7 \pm 0.1
	Mid-aged woodland	128.1 \pm 12.2	3.0 \pm 0.1
Wupatki	Uninvaded grassland	0	-
	Early establishment	10.6 \pm 2.9	2.3 \pm 0.2
	Developing woodland	41.9 \pm 6.2	3.4 \pm 0.1

METHODS

Breeding Birds

At both sites, I established 4 randomly-located, 1-km long transects within each successional stage. To minimize effects of environmental heterogeneity, transects were placed in relatively homogeneous areas >100 ha in size. Each transect contained 5 sampling points spaced 250 m apart. I used distance sampling (Buckland et al. 1993) to estimate breeding bird abundance. Distance sampling is similar to point counts, except that in addition to tallying each bird that is detected, the observer also estimates or measures the linear distance from the point to the bird. These distance data are used to model detection functions, from which one can obtain unbiased estimates of abundance for each species (Buckland et al. 1993). Each point was sampled 3 times during June 1997 and June 1998.

Habitat Sampling

Cover of herbaceous and shrub vegetation was measured on 4 non-overlapping, 50-m point-intercept transects, randomly located within a 100-m radius of each point. Tree density and tree height were measured in a 4-m x 50-m plot centered on the long axis of the intercept transect. Herbaceous vegetation was sampled each year. Trees and shrubs were sampled once in 1997.

Nest Predation

Because of logistic constraints, this portion of the study was conducted only at the Chevelon site. Actual nests occurred at low densities on the study

area and were very difficult to locate, thus I used artificial nests to estimate potential rates of nest predation. While artificial nests may not accurately estimate predation rates on actual nests (Martin 1987, Ortega et al. 1998), they are suitable for comparisons across local habitats or nest sites (Roper 1992).

The artificial nest experiment was a factorial design with 3 independent variables: (1) successional stage; (2) nest placement; and (3) egg type. Artificial nest arrays were left in place for a 14-day period in June 1998, corresponding to the time of egg laying and incubation by local grassland bird species. Twenty 10-cm dia woven grass nests were placed along each transect, at random distances (up to 30 m away from the transect line) and in random directions. Nests were placed in a manner that reflected 2 types of microsites used by common ground-nesting species on the study area: horned lark (*Eremophila alpestris*), lark sparrow (*Chondestes grammacus*), western meadowlark (*Sturnella neglecta*), and eastern meadowlark (*S. magna*). Ten of the 20 nests along each transect were placed within grass clumps, the remaining 10 were placed at the bases of shrubs. Within each type of placement, 5 of the 10 nests contained 2 eggs of exotic finches (*Taeniopygia guttata* and others) and 5 nests contained 2 northern bobwhite quail (*Colinus virginianus*) eggs. The finch eggs approximated the egg size of smaller passerines present on the study area (e.g., horned larks), while the quail eggs were similar in size to those of larger species (e.g., eastern and western meadowlarks).

Data Analysis

Breeding Birds. I used program DISTANCE (Thomas et al. 1999) to model detection functions and

estimate bird density. These analyses were done only for species with adequate sample sizes (≥ 50 detections). I used Jaccard's index (J) (Ludwig and Reynolds 1988) to assess similarity in bird species composition among grassland and woodland transects. This index ranges from 0-1, representing no species in common and total species overlap, respectively. For each transect, I also tallied the proportion of species belonging to 4 nesting guilds (ground, shrub, tree, or tree cavity). Species richness was estimated using the jackknife estimator of Burnham and Overton (1978), implemented in program COMDYN (Hines et al. *in press*). This procedure is an extension of mark-recapture theory, where one estimates number of species instead of number of individuals. The 3 sampling visits done each year represented the "capture" occasions. I used Repeated Measures Analysis of Variance (Neter et al. 1990:1,035) and Scheffe's test to compare species richness and species composition among successional stages. Data from each site were analyzed separately, because of substantial soil and vegetation differences that could affect breeding bird communities. Observed differences were considered significant at $P \leq 0.05$.

Nest Predation. Because the outcome of this experiment was unidirectional and unambiguous. (see Cherry 1998), I did not use inferential statistical procedures to compare predation levels among successional stages, nest placements, or egg types. Results are presented as the proportion of disturbed nests within cells of the factorial design.

RESULTS

Breeding Birds

Species Composition. A total of 22 bird species were detected, 21 at Chevelon and 16 at Wupatki (Table 3). Breeding bird species composition and species richness differed between the 2 study sites. Species richness was lower at Wupatki, where the avifauna was a subset of the species present at Chevelon. Most species occurred in 1 or 2 successional stages at each site. Composition of the breeding avifauna changed dramatically with woodland expansion. Uninvaded grasslands had a relatively simple avifauna dominated by grassland species such as horned larks and meadowlarks. Early establishment woodlands supported grassland species, but also had species associated with shrubby habitat (black-throated sparrow [*Amphispiza bilineata*], loggerhead shrike [*Lanius*

ludovicianus]) as well as woodland species that occupy broad niches (northern mockingbird [*Mimus polyglottos*], Scott's oriole [*Icterus parisorum*]). Developing and mid-aged woodlands had few or no grassland species, and were dominated by woodland species including northern mockingbirds, ash-throated flycatchers (*Myiarchus cinerascens*), common bushtits (*Psaltriparus minimus*), chipping sparrows (*Spizella passerina*), pinyon jays (*Gymnorhinus cyanocephalus*), and scrub jays (*Aphelocoma coerulescens*). Differences in species composition among successional stages were reflected in Jaccard similarity values, which steadily decreased with woodland succession (Table 4). At both sites, extremes of the successional gradient (uninvaded grassland versus developing or mid-aged woodland) had the fewest species in common, whereas woodland stages were most similar to each other.

Nesting Guilds. Nesting guild composition also changed dramatically along the grassland-woodland gradient (Fig. 4). The proportion of ground-nesting species differed ($P \leq 0.05$) among all successional stages at Wupatki, and among all stages except developing and mid-aged woodland at Chevelon ($P \geq 0.05$). Ground-nesters predominated in uninvaded grassland, but decreased sharply with increasing tree density. The proportion of tree-nesting species differed ($P \leq 0.05$) among all stages at Wupatki and among all stages except developing and mid-aged woodland at Chevelon ($P \geq 0.05$). Tree-nesters represented the bulk of the avifauna in developing and mid-aged woodland, but were present in early establishment woodland at both sites (Fig. 4). Cavity-nesting species were relatively uncommon at Wupatki and did not differ among stages ($P = 0.15$). Cavity-nesters made up a greater proportion of the avifauna at Chevelon, where they were most common in developing woodland and mid-aged woodland, and rare or absent in earlier successional stages. The proportion of shrub-nesting species did not vary among stages at either site (Chevelon: $P = 0.053$; Wupatki: $P = 0.054$).

Species Richness. Species richness increased with woodland expansion, ranging from 4.4-19.5 and 3.0-10.5, at Chevelon and Wupatki, respectively (Fig. 5). At both sites, species richness was lowest in uninvaded grassland and highest in developing woodland. Species richness was significantly different ($P \leq 0.05$) between uninvaded grassland and developing woodland at both sites. Species richness was not significantly different ($P \geq 0.05$) in uninvaded grassland and early establishment woodland at Chevelon, but did differ at the Wupatki site. Richness differed in early establishment and developing

Table 3. Occurrence of 22 breeding bird species along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-98. Stages were: S1 = uninvaded grasslands, S2 = early woodland establishment, S3 = developing woodland, S4 = mid-aged woodland.

Species	Chevelon				Wupatki		
	S1	S2	S3	S4	S1	S2	S3
Mourning dove (<i>Zenaida macroura</i>)		√	√	√		√	√
Ash-throated flycatcher (<i>Myiarchus cinerascens</i>)			√	√			√
Cassin's kingbird (<i>Tyrannus vociferans</i>)			√	√			√
Horned lark (<i>Eremophila alpestris</i>)	√	√	√		√	√	√
Scrub jay (<i>Aphelocoma coerulescens</i>)			√	√			
Pinyon jay (<i>Gymnorhinus cyanocephalus</i>)			√	√		√	√
Plain titmouse (<i>Parus inornatus</i>)			√	√			√
Common bushtit (<i>Psaltriparus minimus</i>)			√	√			√
Bewick's wren (<i>Thyromanes bewickii</i>)		√	√	√			
Townsend's solitaire (<i>Myadestes townsendi</i>)						√	
Mountain bluebird (<i>Sialia currucoides</i>)		√	√	√			
Western bluebird (<i>Sialia mexicana</i>)			√	√			
Northern mockingbird (<i>Mimus polyglottos</i>)		√	√	√		√	√
Loggerhead shrike (<i>Lanius ludovicianus</i>)	√	√	√			√	√
Black-throated sparrow (<i>Amphispiza bilineata</i>)		√	√				
Lark sparrow (<i>Chondestes grammacus</i>)		√	√	√		√	√
Spotted towhee (<i>Pipilo erythrophthalmus</i>)			√	√			
Chipping sparrow (<i>Spizella passerina</i>)			√	√			√
Scott's oriole (<i>Icterus parisorum</i>)		√	√	√		√	√
Brown-headed cowbird (<i>Molothrus ater</i>)			√	√			√
Eastern meadowlark (<i>Sturnella magna</i>)	√	√			√	√	√
Western meadowlark (<i>Sturnella neglecta</i>)	√	√			√	√	√
Total number of species	4	11	19	16	3	10	15

Table 4. Similarity of breeding bird species composition along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-98. Values are mean Jaccard's index (*J*) values across years ± SE. Potential index values range from 0-1, representing no species in common and total overlap, respectively.

Study site	Uninvaded grassland	Early establishment	Developing woodland
Chevelon			
Early establishment	0.40 ± .04		
Developing woodland	0.11 ± .01	0.25 ± .01	
Mid-aged woodland	0.03 ± .01	0.13 ± .01	0.57 ± .02
Wupatki			
Early establishment	0.26 ± .02		
Developing woodland	0.13 ± .01	0.52 ± .02	

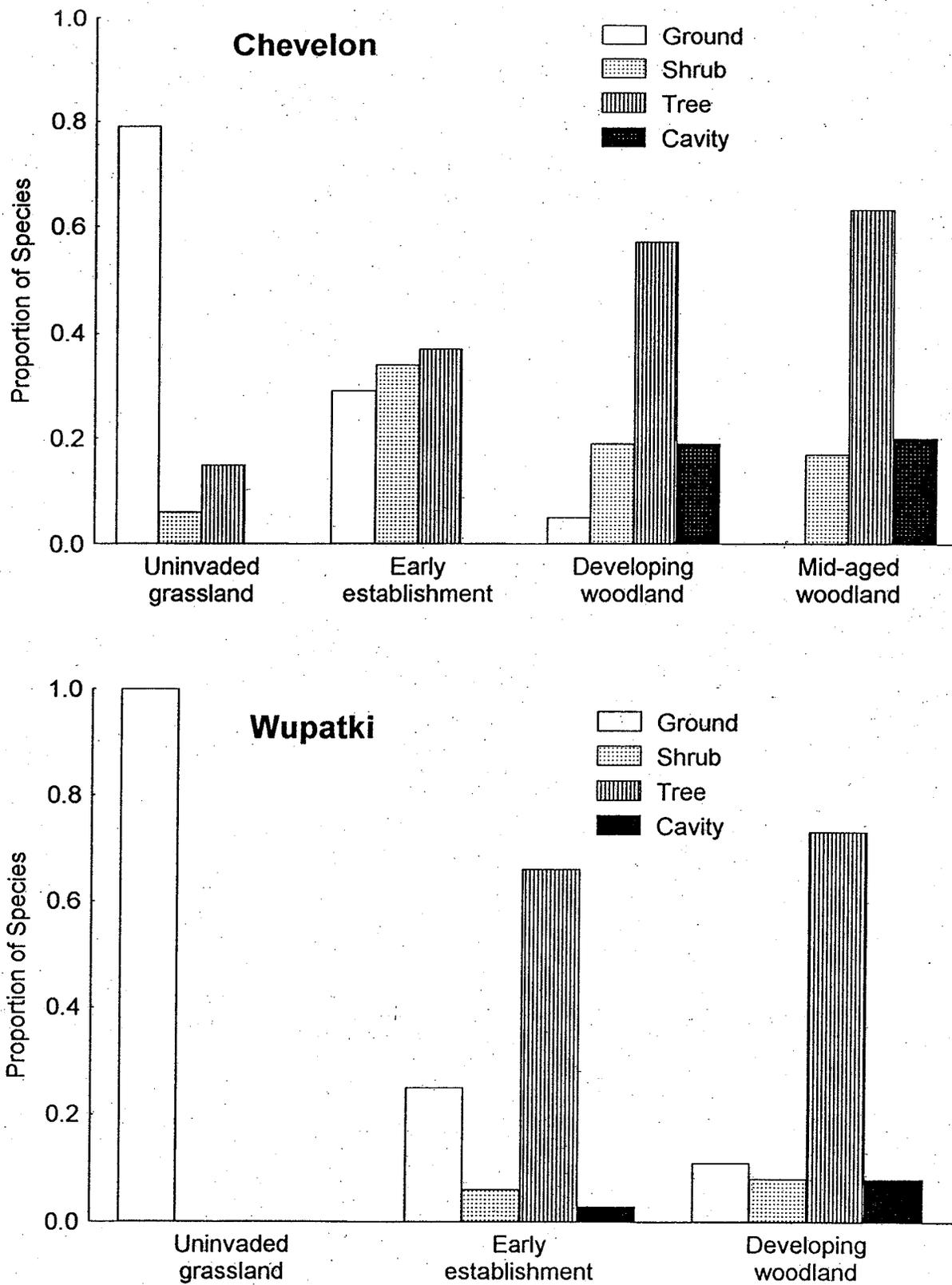


Figure 4. Breeding bird nesting guild composition along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-98.

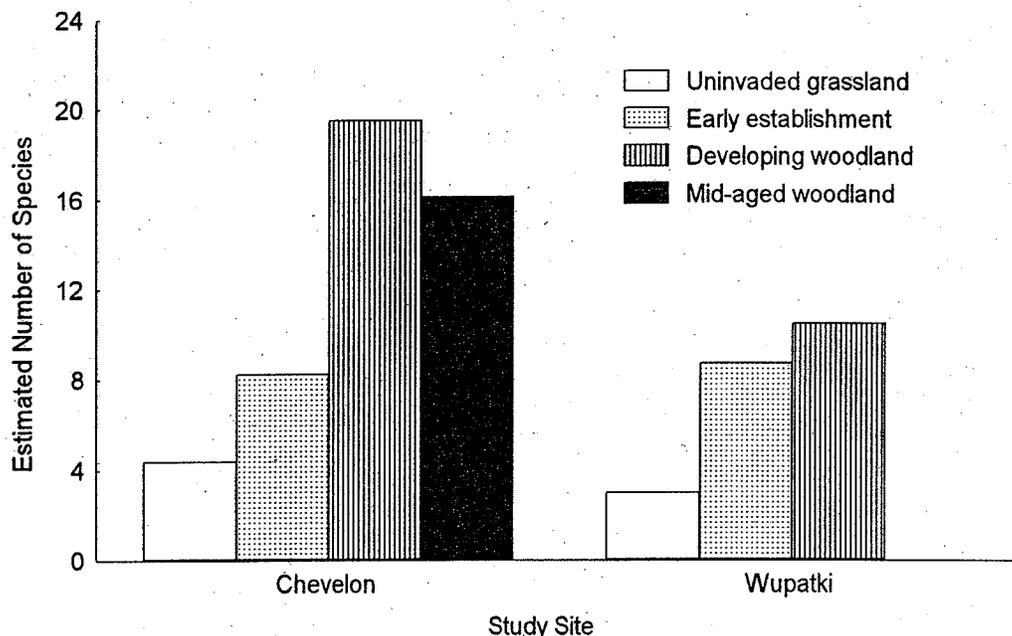


Figure 5. Breeding bird species richness along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-98.

woodland at Chevelon ($P \leq 0.05$), but did not differ at Wupatki. Species richness did not differ between developing and mid-aged woodland at Chevelon ($P \geq 0.05$).

Species' Abundance. The majority of bird species occurred in relatively low numbers; only 12 species had adequate detection sample sizes for density estimation. Three ground-nesting grassland species were most strongly associated with uninvaded grassland and early establishment woodland (Tables 5 and 6). Eastern and western meadowlarks were found in uninvaded grassland and early establishment woodland at Chevelon, and in all 3 successional stages at Wupatki. Abundances of these species were lumped, as it was often impossible to distinguish them in the field, and hybrids are known to occur. At both sites, meadowlarks were most abundant in early establishment woodlands. Horned larks were present in all successional stages except mid-aged woodland, but were most abundant in uninvaded grassland. One ground-nesting species associated with shrubby areas, spotted towhee (*Pipilo erythrophthalmus*) occurred only in developing and mid-aged woodland at Chevelon.

I obtained density estimates for 1 shrub-nesting species (Tables 5 and 6). At Chevelon, lark sparrows were present in all stages and were most abundant in developing woodland. At Wupatki, lark sparrows were found in early establishment and

developing woodland, and were most abundant in the latter.

Six tree-nesting species had adequate sample sizes to estimate density. These species were largely restricted to developing woodland at Chevelon, but several did occur in early establishment woodland at Wupatki (Tables 5 and 6). Common bushtits were present only in developing and mid-aged woodland. Chipping sparrows were equally abundant in developing and mid-aged woodland at Chevelon. Northern mockingbirds were present in all successional stages at Chevelon, but only in early establishment and developing woodland at Wupatki. At both sites, northern mockingbirds were most abundant in developing woodland. At Wupatki, mourning doves (*Zenaida macroura*) had similar abundance in early establishment and developing woodland. Pinyon jays were found only in developing and mid-aged woodland at Chevelon, but were equally abundant in early establishment and developing woodland at Wupatki. Scott's orioles were found in early establishment, developing, and mid-aged woodland, but were most abundant in developing woodland. Cavity-nesting species were restricted to developing and mid-aged woodland. Ash-throated flycatchers were equally abundant in these woodland successional stages at Chevelon and were present in developing woodland at Wupatki. Bewick's wrens (*Thyromanes bewickii*) were found only at Chevelon and were most abundant in mid-aged woodland.

Table 5. Density estimates (birds/ha⁻¹) of 11 breeding bird species along a grassland-juniper woodland successional gradient in northern Arizona, Chevelon study site, 1997-98. Values are means across years ± SE.

Guild Species	Uninvaded grassland	Early establishment	Developing woodland	Mid-aged woodland
Ground-nester				
Meadowlark ^a	0.02 ± 0.01	0.05 ± 0.02	a ^b	a
Horned lark	0.43 ± 0.03	0.37 ± 0.03	0.04 ± 0.02	a
Spotted towhee	a	a	0.08 ± 0.02	0.10 ± 0.01
Shrub-nester				
Lark sparrow	p ^c	0.04 ± 0.01	0.21 ± 0.03	0.03 ± 0.01
Tree-nester				
Pinyon jay	a	a	0.03 ± 0.01	0.03 ± 0.01
Common bushtit	a	a	0.19 ± 0.07	0.74 ± 0.13
Northern mockingbird	p	0.12 ± 0.02	0.25 ± 0.05	0.14 ± 0.04
Chipping sparrow	a	a	0.23 ± 0.03	0.23 ± 0.06
Scott's oriole	a	p	0.06 ± 0.01	p
Cavity-nester				
Ash-throated flycatcher	a	a	0.10 ± 0.02	0.10 ± 0.01
Bewick's wren	a	a	0.07 ± 0.02	0.17 ± 0.02

^a Includes eastern and western species, which often could not be distinguished in the field.

^b a = absent from all transects.

^c p = present on 1 or more transects, but not detected during sampling visits.

Table 6. Density estimates (birds/ha⁻¹) of 9 breeding bird species along a grassland-juniper woodland successional gradient in northern Arizona, Wupatki study site, 1997-98. Values are means across years ± SE.

Guild Species	Uninvaded grassland	Early establishment	Developing woodland
Ground-nester			
Meadowlark ^a	0.06 ± 0.02	0.25 ± 0.05	0.10 ± 0.03
Horned lark	0.33 ± 0.02	0.29 ± 0.02	0.08 ± 0.01
Shrub-nester			
Lark sparrow	a ^b	p ^c	0.21 ± 0.02
Tree-nester			
Mourning dove	a	0.16 ± 0.06	0.13 ± 0.04
Pinyon jay	a	0.06 ± 0.04	0.06 ± 0.02
Common bushtit	a	a	0.04 ± 0.04
Northern mockingbird	a	0.06 ± 0.01	0.23 ± 0.03
Scott's oriole	a	0.02 ± 0.01	0.07 ± 0.02
Cavity-nester			
Ash-throated flycatcher	a	a	0.03 ± 0.01

^a Includes eastern and western species, which often could not be distinguished in the field.

^b a = absent from all transects.

^c p = present on 1 or more transects, but not detected during sampling visits.

Nest Predation

Disturbance rates on artificial nests were extremely high. On the first inspection (7 days after placement), 93% of all nests had been disturbed. Rates of disturbance were similar across all successional stages (uninvaded grassland = 95%, early establishment woodland = 100%, developing woodland = 83%). By the second visit, the overall disturbance rate had increased to 98%, largely due

to predation of previously undisturbed nests on developing woodland transects.

Disturbance rates were independent of nest placement and egg type. Nests placed in grass clumps and under shrubs were heavily disturbed in all 3 successional stages (Table 7). Nests containing finch and quail eggs were subject to similar predation rates, regardless of placement (Table 7).

Table 7. Disturbance rates of artificial nests ($n = 15$ per combination of nest concealment, egg type, and successional stage) along a grassland-juniper woodland successional gradient in northern Arizona, 1998. Values are percent of nests disturbed, rounded to whole percent.

Nest placement Egg type	Uninvaded grassland	Early establishment	Developing woodland
Grass clump			
Finch	87	100	100
Quail	100	100	100
Under shrub			
Finch	100	100	93
Quail	100	100	100

DISCUSSION

Breeding Bird Communities

Differences in the breeding avifauna at the 2 sites likely reflected the influence of vegetative and physical factors. In all successional stages, the Chevelon site had more diverse plant communities and greater structural diversity than did Wupatki. Black volcanic cinders were present over most of the soil surface at Wupatki, creating an extremely hot and potentially unsuitable microenvironment for ground nesting birds. Shrub-nesters represented a minor proportion of the avifauna at Wupatki, where rabbitbrush was the dominant shrub and did not appear to be used by shrub-nesting birds. Shrub nesters were more abundant at Chevelon, which had a more diverse and well-developed shrub component. Fremont barberry was common in early establishment and developing woodland at this site, and was used by several shrub-nesting species. The higher proportion of cavity nesters at Chevelon may have reflected the presence of pinyon pine, an important habitat component for these species in pinyon-juniper woodlands (Balda and Masters 1980).

Woodland expansion had a strong and consistent influence on grassland avifauna. Ground nesting grassland species predominated in uninvaded grassland, but declined as tree density increased. Ground-nesting species made up a very small proportion of the avifauna in advanced stages of juniper invasion. Conversely, the proportion of tree- and cavity-nesting species increased with woodland succession and was highest in developing and mid-aged woodland. Shrub nesters showed little response to woodland expansion, probably because shrubs were relatively sparse on my study areas, and shrub density and shrub size were similar among successional stages. Differences in the

breeding avifauna were most pronounced between endpoints of the successional gradient (uninvaded grassland versus developing or mid-aged woodland). Within woodland successional stages, differences in species composition were proportional to the magnitude of change in the tree component. For example, at the Chevelon site, tree density increased by nearly an order of magnitude between early establishment and developing woodland, and species overlap was low ($J = 0.25$). In contrast, there was only a 4-fold difference in tree density between these stages at Wupatki, and species overlap was much higher ($J = 0.52$). Species richness increased steadily with woodland succession. The breeding bird communities present in advanced stages of woodland invasion (developing and mid-aged woodland) were very similar to those found in higher elevation "true" pinyon-juniper woodlands.

The avian community changes that I observed are consistent with results of previous studies in northern Arizona. LaRue (1994) reported that horned larks and meadowlarks were the dominant breeding species on mined areas revegetated to grassland, whereas juniper-invaded grasslands supported tree-nesting species including northern mockingbirds, loggerhead shrikes, chipping sparrows, and Scott's orioles. Prior breeding bird surveys at Wupatki found 17 species (primarily tree-nesters) at a juniper savannah site, compared to only 8 species at a grassland site (Beatty 1978). Within southwestern pinyon-juniper woodlands, breeding bird diversity and abundance have been positively correlated with tree density and tree size (Masters 1979, Sedgwick 1987, LaRue 1994). Willey (1994) found a positive correlation between bird species richness and vertical complexity of vegetation in grasslands of southern Utah.

Studies in other North American grasslands also have found that invasion or intentional establishment of woody vegetation has substantial effects on breeding

birds. In southern Arizona, invasion of mesquite (*Prosopis velutina*) increased breeding bird species richness, but decreased habitat suitability for several grassland species (Lloyd et al. 1998). Shelterbelt plantings in the Great Plains and midwestern U.S. have been colonized by bird species historically associated with savanna and deciduous forests (Martin 1981, Yahner 1983, Knopf 1994).

The inverse of the woodland expansion pattern that I studied is illustrated in previous studies that examined breeding bird responses to tree removal in Southwestern pinyon-juniper woodlands. Fire, herbicides, and mechanical treatments (e.g., chaining, cabling) have been used to create openings or savanna-like areas dominated by herbaceous and shrub vegetation. Treated areas were dominated by ground-nesting and grassland bird species (Grue 1977, Kruse et al. 1979, LaRue 1994). Diversity was highest in undisturbed woodlands and at woodland edges adjacent to treated areas (O'Meara et al. 1981, Sedgwick and Ryder 1987). Tree- and cavity-nesting species were more abundant in or restricted to untreated or lightly treated woodlands (Sedgwick and Ryder 1987, La Rue 1994).

Responses of breeding birds to woodland expansion likely are driven by linkages between individual species and floristic and physiognomic habitat features (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Cody 1985). The addition of a tree component provides nesting and foraging opportunities for woodland species, but reduces habitat suitability for grassland-obligate birds. The presence of woody vegetation may further influence community structure by altering predation risk for "cover-dependent" versus "cover-independent" bird species (Lima and Valone 1991).

Nest Predation

Predation rates in all successional stages were much greater than reported by artificial nest studies in other grassland and agricultural/old field habitats (Mankin and Warner 1992, Burger et al. 1994, Hendricks and Reinking 1994). My experimental procedures were designed to minimize scent contamination of nests and eggs and to reduce visual cues associated with nest locations (e.g., conspicuous markers or trails). Nevertheless, observer effects may have influenced the outcome of the artificial nest trial.

In this study, predation rates were unaffected by nest placement or egg type. Similarly, Angelstam

(1986) found that horizontal and vertical cover did not affect predation of artificial ground nests at forest-farmland edges in Sweden. Bowman and Harris (1980) noted that spatial heterogeneity of nesting cover was a more important determinant of nest predation than was concealment of the nest. Other studies have reported that quail eggs are "unavailable" to small predators and may underestimate actual predation rates on nests of smaller passerines (Roper 1992). Egg size also can affect the amount of physical evidence (shell material) left after a predation event (Hernandez et al. 1997). Because eggs in my artificial nests were not screened by an incubating female and lacked cryptic coloration, they may have been more detectable to visually-oriented predators than eggs in actual nests.

Artificial nests were not monitored while in place, thus I did not observe predators responsible for nest disturbance. In most instances, sign and tracks left by animals that visited nests were filled in or obscured by blowing dust. At several disturbed nests, however, I found footprints of coyotes (*Canis latrans*) or common ravens (*Corvus corax*). Other potential nest predators were observed on the study area, including badger (*Taxidea taxus*), gray fox (*Urocyon cinereoargenteus*), scrub jay, pinyon jay, and gopher snake (*Pituophis melanoleucus*).

It is often difficult or impossible to identify nest predators based upon nest remains (Larivière 1999); however, some inferences can be drawn from the patterns of nest predation I observed. In most cases (97% of all disturbed nests), 1 or both eggs were missing and shell fragments were not present. This type of disturbance is typical of corvids, snakes, and mammals that remove eggs and consume them elsewhere (Loman and Göransson 1978, Wheeler 1984, Hernandez et al. 1997). Nest disturbance patterns also suggested that different predators visited nests in developing woodland. At disturbed nests in uninvaded grassland and early establishment woodland, nest baskets usually were undisturbed (88% and 87%, respectively). However, in developing woodland, 67% of nest baskets were overturned or moved 1-3 m from their original location. This pattern of disturbance was consistent with the cover-searching behavior of canid predators (Bekoff 1982).

My results suggest that ground-nesting birds in northern Arizona grasslands may be subject to high rates of nest predation, regardless of the level of woodland invasion. Because eggs are available only for a short period of time, predation may be a largely opportunistic phenomenon (Angelstam 1986) and likely attributable to multiple predator species. It also seems that artificial nests are not suitable for studying

levels of nest predation in these habitats. The overwhelming level of disturbance, that was similar across successional stages, egg types, and nest placements, suggests that artificial nests were highly detectable by predators and may not accurately index predation on real nests.

MANAGEMENT OPTIONS

Resource managers have identified woodland expansion as an important issue on southwestern grasslands, particularly on public lands (Loftin et al. 1995). To date, however, restoration efforts in juniper-invaded grasslands have been limited because of high costs and low economic returns. While the grassland bird species I studied are not currently listed as threatened, endangered, or "species of concern," continued expansion of juniper in northern Arizona grasslands will result in additional habitat loss over the long-term and reductions in the numbers of grassland-obligate birds.

My results suggest that removal or reduction of invasive juniper will improve breeding habitat for horned larks, meadowlarks, and other grassland-obligate birds in northern Arizona. Grassland restoration would also benefit other grassland wildlife species. Juniper woodland expansion has been found to decrease habitat quality for pronghorn (*Antilocapra americana*) and increase their susceptibility to predation (Alexander and Ockenfels 1994; R. A. Ockenfels, Arizona Game and Fish Department, personal communication). Anecdotal observations made during this study also suggest that woodland expansion is detrimental to Gunnison's prairie dogs (*Cynomys gunnisoni*). Active prairie dog towns were present on or near all transects in uninvaded grassland, but were absent in all successional woodlands.

When planning and implementing grassland restoration treatments, managers are encouraged to consider the following options:

1. Treatments should be restricted to areas historically occupied by grassland vegetation, as type conversions in higher elevation "true" pinyon-juniper woodlands are expensive and generally have short-lived effects;
2. Priority should be given to sites having a well-established perennial grass component, as artificial seeding or other treatments needed to establish grasses will greatly inflate project cost;
3. A density of >10 juniper trees/ha is an approximate threshold at which habitat suitability for grassland bird species appears to decline, and at which restoration treatments should be considered. Treatment of sites with higher tree densities or larger, mature trees will be more costly or more difficult to implement;
4. Treatments that remove juniper, but that do not damage desirable grasses and understory vegetation (e.g., prescribed fire or hand cutting) are preferable;
5. The introduction or spread of undesirable exotic plants should be avoided; and,
6. Treatments should retain or enhance shrubs that provide song perches and nesting cover for birds (e.g., four-wing saltbush and Fremont barberry). Where shrubs are rare or absent, retaining scattered, small junipers (< 2 m tall) may be desirable.

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