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Species Composition of a Willow Community Relative to Seasonal Grazing Histories in Colorado

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suborbiculata were probably related to its habitat preferences. Backwaters, sloughs, and ox-bow lakes were rarely examined. With the construction of reservoirs, new potential habitat has been created for this species (although often to the demise of many other species) and collecting has been facilitated by accessibility and fluctuating water levels.

I would like to thank Lawrence D. Willis, Dept. of Zoology, Univ. of Arkansas and Charles H. Cope, Dept. Biological Sciences, Wichita State Univ. for their assistance in collecting.—MARK E. GORDON, Dept. of Zoology, Univ. of Arkansas, Fayetteville, AR 72701.

SPECIES COMPOSITION OF A WILLOW COMMUNITY RELATIVE TO SEASONAL GRAZING HISTORIES IN COLORADO—Riparian vegetation in the western United States extends from alpine sites in the Rocky Mountains to below sea level in California (Argus, Univ. Wyo. Pub. 21:1-63, 1957), and is often dominated by a variety of willow (*Salix*) species. In the central Rocky Mountains, willows generally occur as an understory beneath a cottonwood (*Populus sargentii*, *P. angustifolia*) canopy at lower elevations (Harrington, Manual of the Plants of Colorado, Sage Books, Denver, 1954; Marr, Univ. Colo. Studies Ser. Biol. 8, 1961). As elevation increases, cottonwoods disappear and willows occur either in monogeneric stands or form associations with *Betula occidentalis* and *Atnus tenuifolia* (Marr, 1961).

There are 31 known species of willows in Colorado and Wyoming, with most (80%) occurring as shrubs in moist areas (Argus, 1957; Harrington, 1954). This low, shrubby stature increases susceptibility to browsing by ungulates, especially cattle. Browsing can alter the structure and vigor of bushes (Knopf and Cannon, Proc. Wildlife—Livestock Relationships Symp. 10:198-207, Univ. Idaho, For., Wildl. and Range Exper. Sta., Moscow, 1982; Myers, Proc. Montana Chap. Wildl. Soc., In Press; Patten, Ecol. 49:1107-1112, 1968).

Despite the prominence of willows along streams in the Rocky Mountain region (Argus, 1957; Marr, 1961), the impact of browsing upon the species composition of willow communities is unknown. This paper describes the consequences of long-term grazing upon the species composition of a shrub willow community in Colorado.

The study was conducted on Arapaho National Wildlife Refuge (NWR), Jackson County, Colorado. The refuge is located in an intermountain glacial basin, known as North Park (Finch,

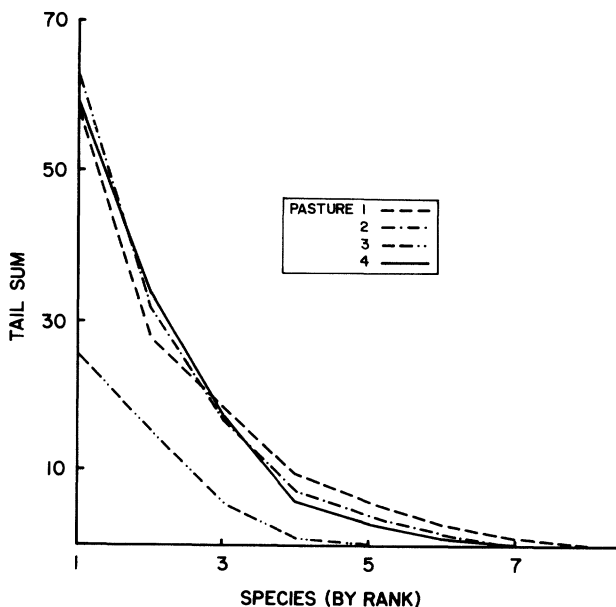


FIG. 1.—Diversity profile of species composition of *Salix* on Arapaho National Wildlife Refuge, Jackson County, Colorado.

TABLE 1.—Floristic composition of the shrub willow (*Salix*) riparian community on Arapaho NWR in Jackson Co., Colorado.

Species	Pasture 1		Pasture 2		Pasture 3		Pasture 4	
	n	%	n	%	n	%	n	%
<i>S. exigua</i>	2	1.9	3	2.4	1	0.8		
<i>S. monticola</i>	31	30.1	46	36.8	12	9.8	16	16.0
<i>S. geyeriana</i>	43	41.7	39	31.2	91	74.6	41	41.0
<i>S. wolfii</i>	4	3.9	4	3.2			3	3.0
<i>S. caudata</i>	9	8.7	12	9.6	6	4.9	26	26.0
<i>S. planifolia</i>	10	9.7	19	15.2	12	9.8	11	11.0
<i>S. pseudocordata</i>	3	2.9	2	1.6			2	2.0
<i>S. bebbiana</i>	1	1.0					1	1.0
TOTAL	103		125		122		100	

Guidebook to the Geology of North and Middle Parks Basin, Colorado, Rocky Mtn. Assoc. Geol., Denver, 1957) which varies from 2400 to 2600 m elevation, and is surrounded by mountain ranges up to 3850 m. Vegetation of North Park and Arapaho NWR is dominated by sagebrush on uplands, with willows, sedges, and grasses occurring in meadows near streams. Weather data from Walden, Colorado (8 km from the study area) indicate that annual precipitation averages 23.2 cm with an average daily temperature of 3.2 C. Frost-free days average 46/year (Smith, Unpubl. Ph.D. dissert., Colo. State Univ., 1966).

The study area comprised portions of the refuge known formerly as the Allard Ranch. A portion of the ranch consisted of 4 pastures along the Illinois River, in which removal of willows had never occurred. The 4 pastures were 105-351 ha in size, and each contained at least 1.5 km of stream. For the purposes of this study, the pastures were numbered sequentially 1-4, moving downstream. These pastures were incorporated into Arapaho NWR in 1969 with the original boundaries intact. Pastures 1, 2, and 3 were traditionally hay meadows and were grazed only during the winter. Pasture 4 was used exclusively for summer seasonal grazing. The seasonal grazing pattern within each pasture had been maintained for at least 50 years prior to the formation of the refuge (E. C. Patten, Manager Arapaho NWR, pers. comm.). Since 1969, the pastures have been intermittently grazed 1 Jul-1 Nov at proper stocking rates (Knopf and Cannon, 1982).

Species composition and distribution of willows were sampled in the 4 pastures during June 1981. At 50 m intervals along the river in each pasture, 100-125 sample points were located perpendicular to the streambank to facilitate selection of a bush for sampling. The distance of sample points from the stream was determined from a random numbers table. The location of sample points did not exceed the width of the shrub willow development. For the bush nearest each sample point, we determined the species and distance from stream.

We used χ^2 and goodness of fit tests to evaluate differences in species composition and richness across the 4 pastures. Species diversity profiles (Patil and Taillie, Pp. 23-48, in Contemporary Quantitative Ecology and Related Econometrics, Int. Coop. Publ. House, Fairland, Maryland, 1979) depicted diversity across the 4 pastures on the basis of evenness and richness.

The sampling effort identified 8 species of willow. The number of willow species were evenly distributed ($\chi^2 = 4.75$; $P = 0.19$) among pastures. The number of individual plants by species varied among pastures $\chi^2 = 74.7$; $P < 0.01$), at least for those species (*S. geyeriana*, *S. monticola*, *S. caudata*, *S. planifolia*) occurring in sufficient numbers to be tested for independence.

Diversity profiles (Fig. 1) indicated that pastures 1, 2, and 4 were similar in species richness and evenness. Pasture 3 had fewer species of willows and was less diverse than the other pastures. The simplicity of the willow community in pasture 3 was due largely to a shift in evenness among the 5 species present, with a dramatic increase in dominance by *S. geyeriana* (Table 1).

Data from all pastures were combined to evaluate the spatial distribution of the 4 major species relative to distance from stream edge. Distance-from-stream measurements were lumped by 5 m intervals by species. *Salix geyeriana* became more dominant away from the stream, while percentages of *S. monticola*, *S. caudata*, and *S. planifolia* declined (Fig. 2).

In a related study of Arapaho NWR (Knopf and Cannon, 1982), the pastures (2 and 3) with a history of winter grazing were found to be structurally similar, and considered to be in "good"

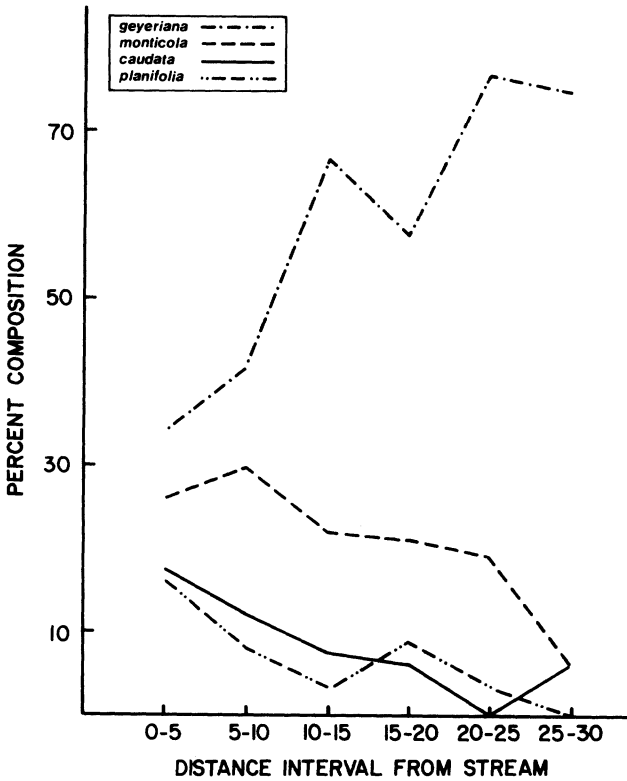


FIG. 2.—Percentage composition of *Salix geyeriana*, *S. monticola*, *S. caudata*, and *S. planifolia* by distance interval from stream.

condition. In contrast, pasture 4 with a history of summer grazing was in “poor” condition, and differed significantly for all structural variables measured. Bushes in pasture 4 were larger, more decadent, and more widely spaced. The width of riparian development was also significantly reduced from that in winter-grazed pastures.

If summer or winter seasonal grazing had affected the composition or diversity of the willow community, we would expect a pattern among the pastures equivalent to that found for structure (i.e., pastures 1, 2, and 3 similar in composition and pasture 4 significantly different). Instead we found pasture 4 to have a diversity profile similar to pastures 1 and 2, in spite of the structural differences inflicted by summer seasonal grazing. We conclude that seasonal grazing in winter or summer had little or no effect on composition or diversity of the willow community.

We then suspected that historical removal of water from the Illinois River for irrigation might explain the species composition pattern in the willow community. In addition to several irrigation ditches upstream from the refuge, 2 ditches originate in pasture 3, and 1 in pasture 4. These water diversions for irrigation have affected stream flow on the Illinois River for nearly 100 years, typically causing stream flow through the 4 pastures to nearly cease by mid-to-late July (E.C. Patten, Manager Arapaho NWR, pers. comm.). The similarity in composition of pastures 1, 2, and 4 however, did not follow this pattern of increasing water diversions downstream. Thus, we also concluded that the observed species composition of the *Salix* community was independent of seasonal practices of stream dewatering.

A significant physical feature of the study area was a division of the stream into 2 widely spaced channels (up to 0.8 km) immediately upon entering pasture 3. The 2 channels rejoined immediately prior to entering pasture 4. Although not measured, stream flow within either channel was noticeably less than that in the single channel, both upstream and downstream.

Because species composition of willow communities can follow soil moisture gradients perpendicular to streams (Patten, 1968), we suspect that available soil moisture perpendicular to the 2 channels in pasture 3 is relatively less than in the adjoining pastures (2 and 4) with single stream channels.

Growth of *Salix* is extremely sensitive to available soil moisture (Albertson and Weaver, Ecol. Monogr. 15:393-433, 1945; McLeod and McPherson, Bul. Torrey Bot. Club 100:102-110, 1973), in addition to exhibiting specific requirements for germination (McLeod and McPherson, 1973). Based on our data and circumstantial evidence, we suspect that the species composition and distribution of willows in pasture 3 relative to pastures 1, 2, and 4 are the result of an altered soil moisture regime which has influenced the historical development of the *Salix* community.

We thank E. C. Patten, and W. J. Wilson of Arapaho National Wildlife Refuge for permission to work on the refuge. We also thank H. O. Krueger for field assistance and C. Feddema for assistance with identification of willow species. R. Engeman provided statistical advice. J. K. McPherson and J. L. Oldemeyer reviewed the manuscript.—RICHARD W. CANNON and FRITZ L. KNOPF, *Denver Wildlife Research Center, U.S. Fish and Wildlife Service, 1300 Blue Spruce Drive, Fort Collins, CO 80524* (present address of RWC: *Fish and Wildlife Research Center, Missouri Department of Conservation, 1110 College Avenue, Columbia, MO 65201*).

FIELD OBSERVATIONS OF LARVAL DEVELOPMENT AND AGGREGATION OF THE RANGE CATERPILLAR, *HEMILEUCA OLIVIAE* COCKERELL (LEPIDOPTERA: SATURNIIDAE).—The range caterpillar is an inhabitant of grasslands in central and northern New Mexico and adjoining areas of Texas, Colorado and Oklahoma. Wildermuth and Caffrey (USDA Bull. 443:1-12, 1916) give a general account of larval development and Ainslie (USDA Bureau Entomol. Bull. 85:59-96, 1910) describes the gregarious habits of the early instars. Hansen et al. (Environ. Entomol. 11:355-360, 1982) present field life table data for all developmental stages. However, there have been neither field measurements of instar duration nor field studies quantifying the reduction of the larval masses. In this study, we investigated these activities under natural conditions.

This work was part of a comprehensive field study on larval behavior which was conducted on two sites 10 km south of Springer, NM. In the summer of 1979, hourly day-time observations on at least two successive days per week were made from the time of hatch to pupation (May to September). For each observation, the number of individuals in every larval mass and their instar were recorded. Instar duration was estimated by taking the mid-points between the peaks of the daily frequency distribution of instars and assuming these were the beginning and end of each respective stadium.

Larval Development.—Stadia lengths estimated from daily instar frequencies were similar for both sites (instar-I: Site 1 — 6.5 da., Site 2 — 8 da.; instar-II: Site 1 — 11 da., Site 2 — 12 da.; instar-III: Site 1 — 9 da., Site 2 — 7 da.; instar-IV: Site 1 — 8.5 da., Site 2 — 10 da., instar-V: Site 1 — 22 da., Site 2 — 23 da.; instar-VI: Site 1 — 35 da., Site 2 — 34 da.). When frequency estimates were compared by chi-square tests to actual measurements of time between molts of different stadia for several larvae, there was no significant difference.

The long stadia-V and -VI allow larvae time to spread and to feed more effectively, but the very short stadia-III and -IV almost seemed fortuitous. However, all the estimated stadia lengths were similar to those observed from other populations in northern NM (Hansen et al., 1982). Also, Watts and Everett (NM Agric. Sta. Bull. 646:1-32, 1976) showed short duration of stadia-II to -IV (ca. 8 da.) for larvae hatching in mid-July. In the armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae), instar duration decreases with rise in temperature up to 29°C (85°F) (Guppy, Can. Entomol. 101:1320-1327, 1969). The middle stadia may be intrinsically short and further decreased by the influence of warm summer temperatures.

Larval Aggregation.—The gregarious behavior of early instars of the range caterpillar was described by Ainslie (1910). In our studies, we measured the reduction of larval mass size during development (Fig. 1). The rate of reduction of the first five instars produced a sigmoid curve. Initially, the larval masses were larger at Site 1, but by instar-III the average size was about the same for both sites. After the next molt, larvae were generally solitary. The most numerous mass observed for instar-I was 55 larvae and for instar-II 58 larvae.

Members of a larval mass did not necessarily come from the same egg mass. Marked individuals showed that masses sometimes merged and then divided into clusters with different larvae.