BEAVER-COTTONWOOD INTERACTIONS AND BEAVER ECOLOGY IN BIG BEND NATIONAL PARK

By

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BEAVER-COTTONWOOD INTERACTIONS AND BEAVER

ECOLOGY IN BIG BEND NATIONAL PARK

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INTRODUCTION

This thesis is a manuscript written in a format suitable for submission to WILDLIFE MONOGRAPHS. The manuscript is complete without additional supporting material and is in compliance with the Graduate College of the Oklahoma State University.

BEAVER-COTTONWOOD INTERACTIONS AND BEAVER ECOLOGY IN BIG BEND NATIONAL PARK

INTRODUCTION

Beaver (*Castor canadensis*) have long been of interest for their economic importance as a furbearer and have been among the most frequently studied of North American mammals. However, studies of beaver ecology and management (Bradt 1938, Aldous and Harris 1946, Yeager and Rutherford 1957) have been conducted primarily in northern ecosystems. Few studies of beaver ecology have been conducted in the Southwest, and of these, most have been done on high altitude, clear-water streams where population densities were greatest (Jackson 1953, 1954, Huey 1956). Until recently, little attention has been given to populations occupying marginal habitat along sediment-laden, low altitude rivers, such as the Rio Grande in Texas. Schmidly and Ditton (1976) described floodplain habitat along the Rio Grande in southwestern Texas and Boeer and Schmidly (1977) investigated the mammalian fauna of the riparian corridor of the Rio Grande in Big Bend National Park, Texas. Connor and Feeley's (1976, unpubl. rep., Big Bend National Park, Texas) preliminary observations of the distribution and food habits of Mexican beaver (*C. c. mexicanus*) and damage by beaver to cottonwoods (*Populus* spp.) in the Park represent one of the few efforts to date to investigate beaver in this ecosystem.

A noticeable decrease in the number of cottonwood trees and the lack of information about the effects and extent of beaver use of cottonwoods along the Rio Grande floodplain in Big Bend National Park has concerned Park officials. National Park Service policy for plant and animal resources states, "Native environmental complexes will be restored, protected and maintained, where practicable, at levels determined through historical and ecological research of plant-animal relationships..." (USDI 1970, p. 17). The Resource Management Division of Big Bend National Park recognized the need for more information on beaver-cottonwood interactions and the potential effects of beaver use of cottonwoods in its recent Resource Management Plans report.

This study was initiated to provide information on beaver and cottonwood resources in Big Bend National Park. Research was concentrated on beaver use of native cottonwood stands in the Park. Food habits, den site characteristics, and other aspects of beaver ecology were investigated to fill gaps in the knowledge of beaver ecology in southwestern riparian ecosystems. The results of this study will provide a base for management of beaver and cottonwood resources in Big Bend National Park and similar habitats in the American Southwest.

Specific objectives were:

1. To locate, map, and characterize physical parameters of native cottonwood and willow (Salix spp.) stands along the Rio Grande in Big Bend National Park;
2. To determine locations of beaver activity and estimate population size of beaver in the Park;
3. To assess beaver use of native cottonwoods;
4. To determine food habits of beaver in the Park; and
5. To characterize beaver den sites.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the following individuals and agencies who made important contributions to the study. Without the financial support provided by Big Bend National Park, National Park Service - Southwest Region, the Oklahoma Cooperative Wildlife Research Unit, and the Rob and Bessie Welder Wildlife Foundation, this study would have not been possible.

Dr. John Bissonette, my adviser, provided leadership, support, and advice in all phases of the study. Drs. Edward Sturgeon and Thomas Gavin served on the graduate committee and aided in formulation of the research proposal. Dr. James Shaw substituted for Dr. Gavin during the oral defense. Dr. William Warde assisted with statistical analysis. Drs. James McPherson and Ronald Tyrl aided in identification of cottonwoods. I profited from discussions with Dr. Charles Tauer.

Many personnel of Big Bend National Park were helpful in various phases of the study. Resource Management Specialists Michael Warren and Michael Fleming aided in procurement of information and gave advice. Resource Management Technician Kathy Hambly patiently put up with my requests for information from Park files and faithfully sent information to me after I left the Park. Interpreter Robert Devine deserves special thanks for reporting beaver activity and taking an active interest in the research. All members of the Ranger Division were helpful. Special thanks must go to George West, Rich Simmons, Jay Liggett, and Dave Griese of Rio Grande Village and Ron Sprinkle, Rudy Carrasco, Len Weems, and Don Revis of Castolon for providing transportation along the river. Marshall Smith of the USDA also provided invaluable assistance with transportation on backcountry roads. Felix Hernandez was a source of information and stimulating conversation. James Chambers provided information on cottonwoods in the Park.

Bruce Leopold provided invaluable friendship, companionship, and advice during the field season and helped identify and age cottonwoods. I benefited from conversations with Danny Swepston of Texas Parks and Wildlife Department.

Very deepest thanks go to Judy Gray who faithfully sent mail, kept me posted on Unit activities, and performed a number of tasks for me while I was in the Park.

I am forever grateful to my friends Gordon and Mary Batcheller who gave me advice, support, friendship, and many meals when I needed them most.

I would like to express my warmest feelings toward all of my friends in Big Bend National Park who helped make my stay enjoyable and especially to the John Pearson family, my close friends and "family" in the Park.

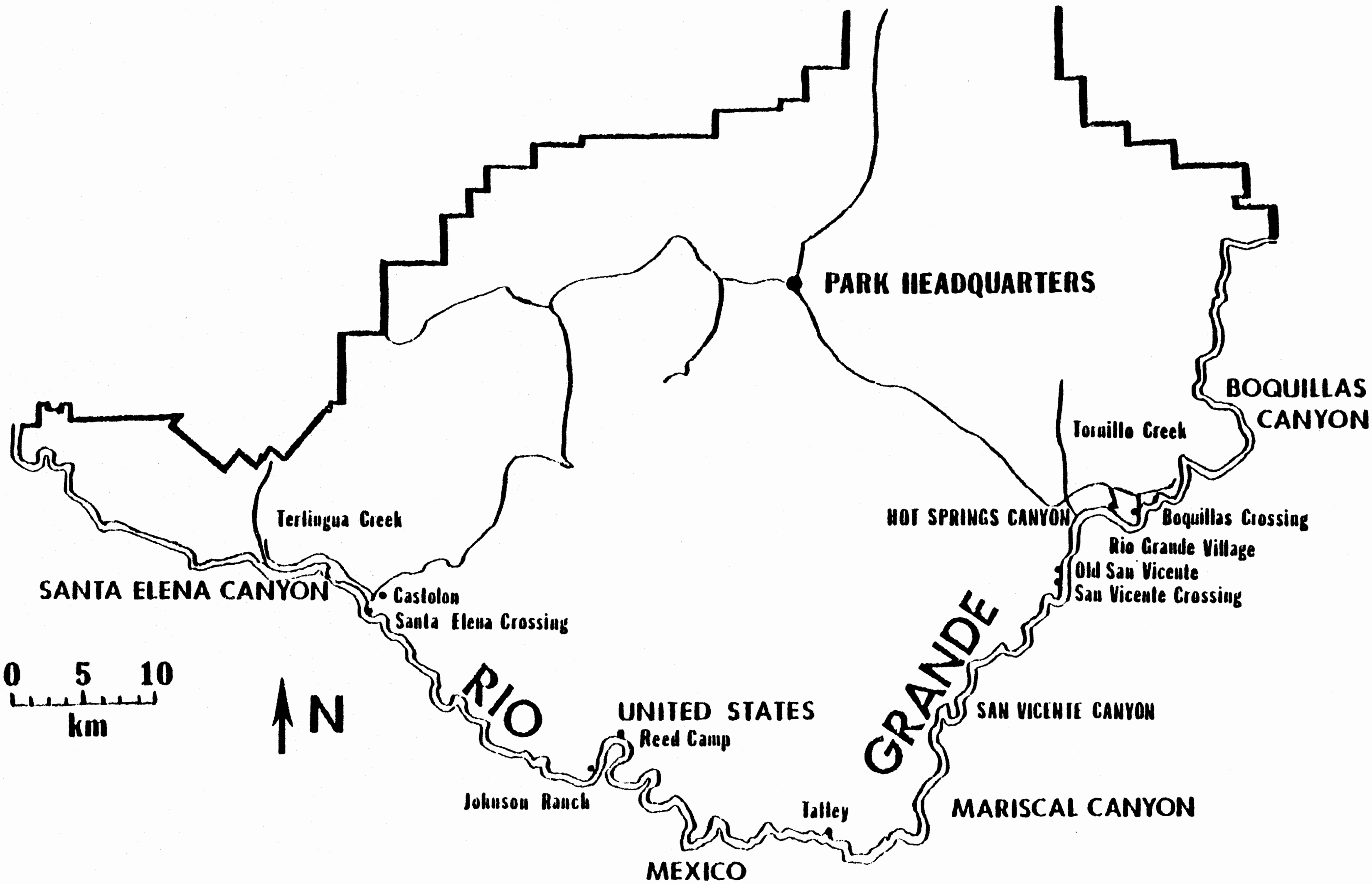
STUDY AREA

Field work was conducted along 131 km of the Rio Grande between Santa Elena and Boquillas Canyons in Big Bend National Park in southwestern Texas (Fig. 1). The 172 km of river bordering the Park and approximately 221 additional km east of the Park are under the jurisdiction of the U.S. Department of the Interior, National Park Service. The natural resources within the Park have been protected since 1944.

The Park is in a subtropical belt of high pressure that produces xeric climates around the world. It has been assigned to the Chihuahuan biotic province and is composed of mountain, lower foothill, desert

Fig. 1. Big Bend National Park, Texas.

BIG BEND NATIONAL PARK



flatland, and river bottom biotic zones (Borell and Bryant 1942). The elevation at the river is 660 m above sea level at Santa Elena Canyon and 520 m at Rio Grande Village.

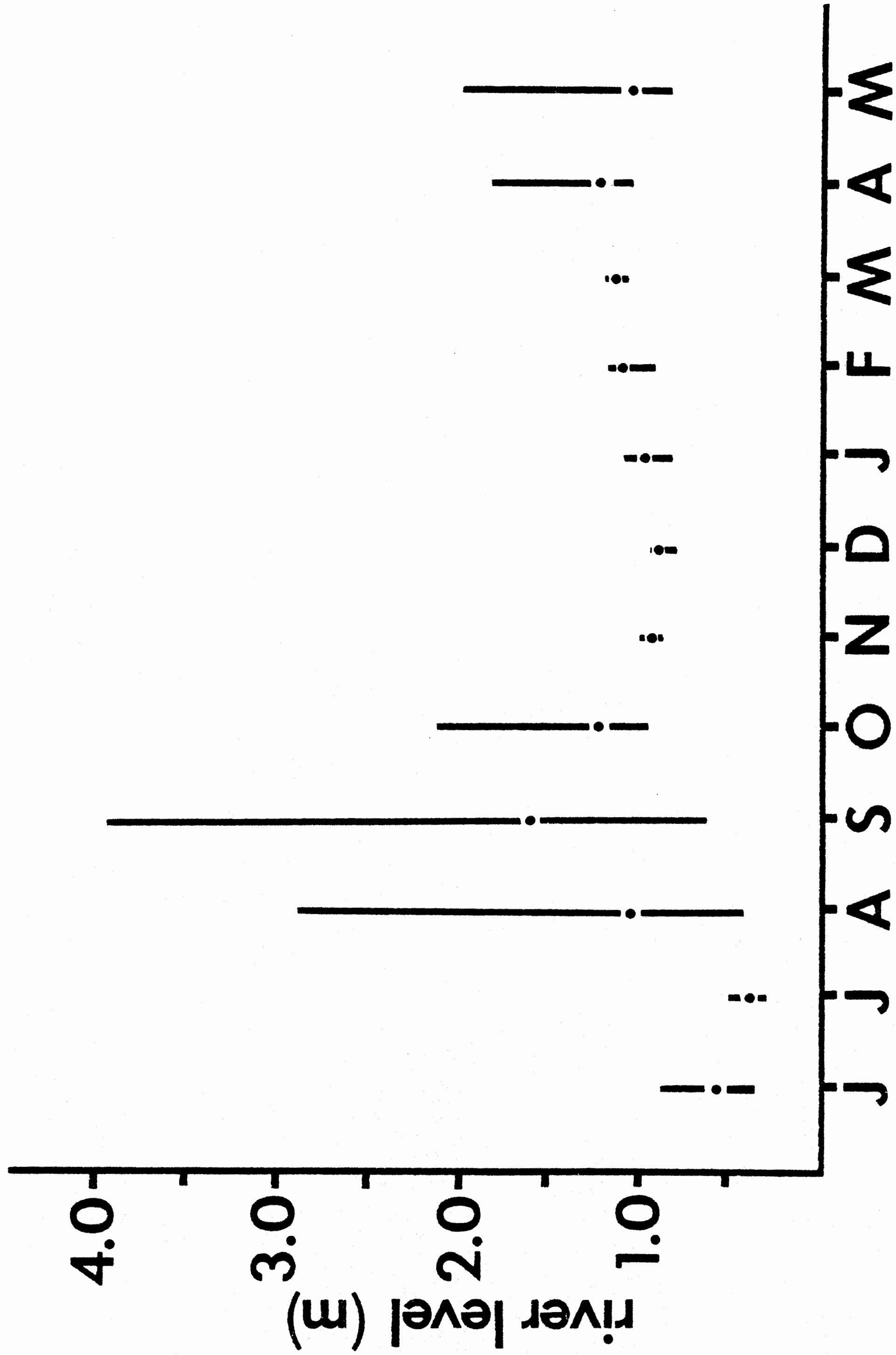
The rainy season is from May to October (Wauer 1973, p. 8), but rain may fall at any time of year. The average rainfall for the floodplain is approximately 25 cm. Abrupt topographic features of the region are probably responsible for some irregularities in rainfall and low elevations along the river usually result in higher than normal humidity and temperature than in the rest of the Park.

There are large variations in air temperatures along the Rio Grande. During the study period daily highs ranged 5–47°C and daily lows ranged -5–28°C. June was the hottest month. The temperature of the river 1 foot below the surface reached a high of 32.5°C in July and a low of 11°C in November. Changes in river temperature over a 24-hour period ranged 2–6°C.

River levels fluctuated widely (Fig. 2). A low of 0.33 m and a high of 3.95 m were recorded at the staff gauge in Rio Grande Village. The average river level during the study period was 1.01 m. The highest monthly average was 1.60 m in September and the lowest was 0.56 m in June. Large ingresses of water after summer rains caused dramatic changes in river level over short periods of time. The greatest rise in river level over a 24-hour period was 2.03 m.

Most of the water in the Rio Grande has been drawn off for irrigation by the time it reaches El Paso. An environmental assessment for the general development plan of the Rio Grande (United States Department of the Interior 1980) estimated 75 percent of the water in the Rio Grande in Big Bend National Park originates from the Rio Conchos,

Fig. 2. Monthly river level means and extremes (m) for the Rio Grande, June 1980 - May 1981, Rio Grande Village, Big Bend National Park, Texas.


river level (m)
4.0
3.0
2.0
1.0
J
J
A
S
O
N
D
J
F
M
A
M

which drains a large watershed in northern Mexico.

The average width of the river in the Park is 30 m (Connor and Feeley unpubl. rep.). It is narrower in the large canyons. The depth is variable, but is usually 1.0 m or less. Current speed is also variable and depends on the amount of the water in the river and the width of the channel. The fastest flowing water is found in the narrow bends of the river.

The river is always muddy with near zero visibility beneath the surface. Heavy metal concentrations, such as, mercury, are not significant problems at present, but could become so if old mines near the river are reopened. The major water quality problem at present is the presence of DDT and its metabolites originating from fertilized farmland runoff in Mexico.. DDT levels are high near Presidio where the Rio Conchos enters the Rio Grande, but current DDT levels in the Rio Grande in the Park are not appreciable (USDI 1980).

The valley of the Rio Grande in Brewster County only occasionally widens to form alluvial deposits that support a rich growth of several plant associations. Santa Elena, Mariscal, and Boquillas, the 3 major river canyons in the Park, are narrow and steep-sided, leaving little room for vegetative growth or for formation of distinct plant associations. Santa Elena and Mariscal Canyons are approximately 12 km long, very narrow, and have nearly vertical walls as high as 450 m. Little soil has been deposited in these canyons and vegetation is sparse. Boquillas Canyon is 29 km long and its walls are not nearly as steep nor as high as those in Santa Elena and Mariscal. Much more vegetation is present.

Two small river canyons are located between Mariscal and Boquillas

Canyons. San Vicente Canyon is 7 km long and is narrow. Its walls are vertical, approximately 100 m high. Little vegetation is present. Hot Springs Canyon is 2.5 km long. Its walls are 30 m high. Some vegetation grows on several large gravelbars. Large trees are uncommon in all river canyons.

The riverbank association along the Rio Grande was "... not characterized by any definite group of plants. Occasionally, mesquite, baccharis, willow, or cottonwood overhang the water, but usually there are exposed flats of silt and coarse gravel between the vegetation and the river. No plants grow on these flats since they are subject to frequent flooding." (Denyes 1956, p. 295). Schmidly and Ditton (1976) reported general impressions of significant vegetational changes in riparian habitats of Big Bend National Park over the past 30 years, including a tremendous increase in tamarisk (*Tamarix* spp.), an introduced phreatophyte, that appeared to be replacing the native cottonwoods and willows. The baccharis (*Baccharis* spp.) association that Denyes (1956) found commonly in the fine sandy loams was recognizable at few places. It appeared to have been replaced by a mixed mesquite (*Prosopis juliflora*)-tamarisk-bermuda grass (*Cynodon dactylon*) association. Qualitative observations of the study area revealed common reed (*Phragmites communis*) and giant reed (*Arundo donax*) and tamarisk as dominant plant species. Cottonwood, willow, and baccharis were localized and uncommon.

The Rio Grande is part of the international boundary between the United States and Mexico. Land use practices on the Mexican floodplain adjacent to the Park have severely modified the vegetation. Overgrazing is common, resulting in poor ground cover. Tamarisk, mesquite, common and giant reed, and other vegetation unpalatable to livestock are dominant plant species. Cottonwood and willow can be found at few places. Where they do occur cattle have browsed them heavily.

METHODS

Locating and Characterizing Cottonwood, Willow, and Beaver Resources

Locations of native cottonwood and willow stands on the Rio Grande floodplain (U.S. side) were mapped during canoe and raft trips on the river and from the River Road, a 77 km unimproved dirt road paralleling the river between Castolon and the mouth of Tornillo Creek. Native cottonwoods were classified taxonomically after examination in Spring 1981. Cottonwoods from the Terlingua Abaja site were identified in Fall 1981. Additional data were collected at the cottonwood stands. Height, age, diameter at breast height, and distance from the river were measured for each cottonwood tree in 4 stands. Trees with rotten centers (16.7%) were not included in mean age calculations. Numbers of root sprouts and epicormic shoots were tallied at each tree in the 4 stands. Stump collar shoots were classed as epicormic shoots. Human and livestock disturbances and tamarisk invasion at cottonwood sites were classed as low, moderate, or high in order to evaluate their effects on cottonwood regeneration and on beaver activity. Overall stand condition was evaluated. Evidence of human disturbance included campsites, litter, firewood cutting, and travel through the area. Livestock disturbance was noted by presence of animals, trails, feces, and browsed vegetation. Tamarisk invasion was documented by noting relative density of tamarisk in each stand.

Willow stand density was classed as high, medium, or low. Ten percent of each of 3 stands was sampled to determine stand composition.

All woody stems were tallied within 1-m wide strip transects placed perpendicular to the river. A complete compilation of trees felled by beaver was made in 2 stands.

Areas of beaver activity were mapped during canoe and raft trips. All signs of activity including observations and presence of scent mounds, feeding sites, runways, tracks, and dens, were used to delineate boundaries of the activity areas.

Observing and Censusing Beaver

Because of their secretive nature, nocturnal habits, and the remoteness of colony sites, direct observation of beaver was often difficult. Most observations were made during river float counts although some were made from vantage points on land. Two methods were commonly used to locate feeding beaver. First, I canoed or floated in an innertube through the beaver colony staying close to the dense vegetation overhanging the bank. Often, beaver did not detect me until I was very close. The beaver's most common response to the canoe was to swim away from the bank. They were then easily seen. Second, beaver could sometimes be located by the sound of their gnawing on woody stems. These locations were observed until either the beaver swam from the bank or I approached in an effort to flush the animal. Tail slaps were the most reliable indication of beaver activity. However, other colony members often became wary after a tail slap and the observation of more than 1 beaver was rare. Several times beaver were induced to leave their dens by slapping the water with a canoe paddle near the den entrance.

A population estimate of beaver in Big Bend National Park was made. Five beaver colonies were observed regularly and exact numbers of beaver were determined. Observations at other colonies yielded a minimum number for the Park. Estimates of beaver numbers for each activity area were made by evaluating the habitat of each area and comparing it with the habitat and known density of beaver in the 5 intensively studied colonies.

Food Habits

Feeding sites of beaver were located and data on food items were collected. Damage to cottonwoods was classed into distinct categories and assessed at 7 stands. The number of trees damaged by beaver at Terlingua Abaja was not quantified. Five colonies were selected on a basis of known boundaries and ease of accessibility for intensive study of food habits. After an initial marking of all tree stumps, each colony was visited biweekly and data were collected on feeding activity. The floodplains adjacent to the colonies on both sides of the river were searched from land and water. All woody vegetation cut by beaver was recorded by locating unmarked stumps. Species, diameter, and distance from the river were recorded for each stump. Stump tops were marked with paint to prevent recounting.

Bark weights were determined for the most commonly cut 1-cm diameter classes of the 3 most common food items. A random sampling scheme was devised and 5 trees from each diameter class were cut in a stand in Rio Grande Village. Willows 0-6 cm, tamarisk 0-3 cm, and baccharis 0-4 cm diameter were sampled. Each tree was stripped of all bark. Leaves and stems < 0.2 cm diameter were not included in the bark sample. Bark was air dried for 2 weeks and weighed on a gram balance to the nearest 0.5 g.

Qualitative notes of other foods eaten by beaver were made by collecting vegetation washed up on the riverbank, observations of feeding activity, and by following tracks and runways to feeding sites not regularly monitored for feeding activity.

Locating and Characterizing Den Sites

I located den sites of beaver by walking and floating close to the riverbanks and searching for den entrances. Dens were occasionally located by observing beaver returning to their dens at the end of activity periods. Ten km of river between the mouth of Santa Elena Canyon and Castolon and 16 km of river between the Old San Vicente river site and Boquillas Canyon were searched intensively for dens during periods of low river level.

Structural characteristics of the dens and their immediate surroundings were noted at each site. Parameters measured were size of opening, depth of burrow, current speed, position of burrow entrance on the bank, soil type, position on river, and dominant vegetation. The number of dens used during the study period was recorded for 5 colonies.

Weather Data

Climatological data were collected on a regular basis. The National Park Service recorded daily high and low temperatures and river levels at Rio Grande Village. I recorded air and river temperatures hourly for a 24-hour period at Rio Grande Village once a month from July 1980 through April 1981.

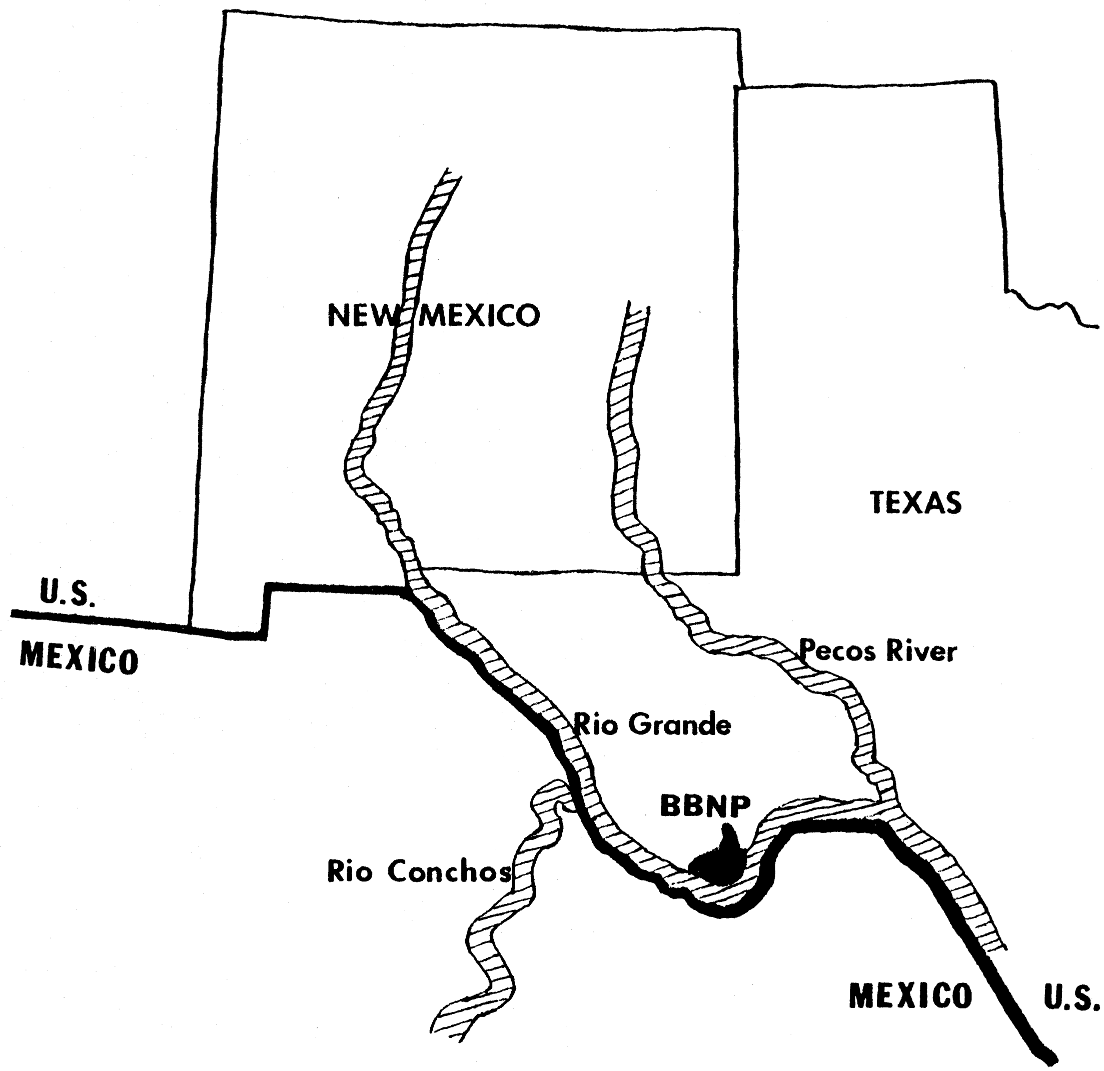
HISTORICAL BACKGROUND

Mexican Beaver

Beaver populations were greatly reduced throughout much of North America as the result of extensive trapping in the 19th century. Trapping and habitat destruction due to grazing continued to depress beaver numbers throughout the United States, including the Southwest during the early part of the 20th century (Leopold 1959, p. 380). Recent efforts at reintroduction have been a wildlife management success story (Scheffer 1927, Atwood 1938). Mexican beaver were not completely extirpated from their range. The rugged terrain coupled with sparse population densities probably contributed to the survival of this subspecies. No reintroductory transplants to or from the range occupied by the Mexican subspecies have been documented (Swepston 1976). Present populations appear the result of natural growth and dispersal.

Bailey (1927) described the Mexican beaver and its distribution on the Rio Grande and associated waterways in New Mexico, southwestern Texas, and northern Mexico. Findley and Caire (1977) reported this subspecies to occur sporadically on the Rio Conchos, Rio Grande, Pecos River, and their tributaries (Fig. 3). Scattered colonies of beaver were reported along most of the length of the Rio Grande in Texas (Lay 1944) and in Big Bend National Park "...from the mouth of Santa Helena [sic] Canyon to the mouth of Boquillas Canyon..." (Borell and Bryant 1942, p. 28). Beaver were once abundant in Terlingua Creek, a tributary of the Rio Grande in the Park (Gillette 1933). Although Bailey (1905) noted beaver along the Rio Grande in western Texas and found signs of beaver activity where the Park exists today, Taylor (1944) and Wauer (1980) did not include beaver in their faunal reports of Big Bend National Park. In the 1930's beaver pelts were occasionally brought to Johnson Ranch, a fur-trading post on the Rio Grande (Maxwell 1967, p. 60). Swepston (1976) estimated 300-500 beaver inhabited the Rio Grande in Brewster County, an area that includes the Park. Most recently, beaver were reported as uncommon along the

Fig. 3. Distribution of Mexican beaver in North America (after Findley and Caire 1977).



DISTRIBUTION OF MEXICAN BEAVER

Rio Grande in Big Bend National Park (Connor and Feeley unpubl. rep., Boeer and Schmidly 1977).

Native Cottonwoods

Once common, few cottonwood trees grow along the Rio Grande and its tributaries in Big Bend National Park today. Gillette (1933) described an area along Terlingua Creek in 1885 as a bold, running stream with many cottonwoods. Denyes (1956) claimed that cottonwoods once overhung the water along much of the Rio Grande.

The reasons for the decrease in cottonwood numbers are not fully known. Human influence and the invasion of tamarisk throughout the Southwest are often cited factors responsible for the decrease (Schmidly and Ditton 1976). Cottonwoods were cut for building purposes during the settlement of the Big Bend (Wauer 1980, p. 24). Although trees in the Park have been protected since 1944, farmers continue to use cottonwoods, and livestock browse cottonwood shoots on the Mexican floodplain. Destruction of riparian vegetation by trespass livestock is still a problem in Big Bend National Park.

Cottonwood numbers have decreased since tamarisk was introduced into the western United States in the late 1800's (Robinson 1965). Tamarisk is well adapted for dry and saline soils (Carleton 1914), but also grows rapidly on silt plains in areas frequently inundated by flooding and in overgrazed areas (McAtee 1914, Fosberg 1967). Seeds of cottonwoods also pioneer the silt plains. Tamarisk often outcompetes cottonwood on the silt plains because it becomes established and grows so quickly (Munns 1950).

RESULTS

The Cottonwood Resource

Locations

I located 8 sites along the Rio Grande in Big Bend National Park where native cottonwoods still exist in addition to cottonwood nurseries at Cottonwood Campground in Castolon and in Rio Grande Village (Fig. 4). The trees in the nurseries were planted by the National Park Service (James Chambers, pers. comm.) and are not native stands. Cottonwoods are present at several river sites in Mexico, most commonly near small Mexican ranches.

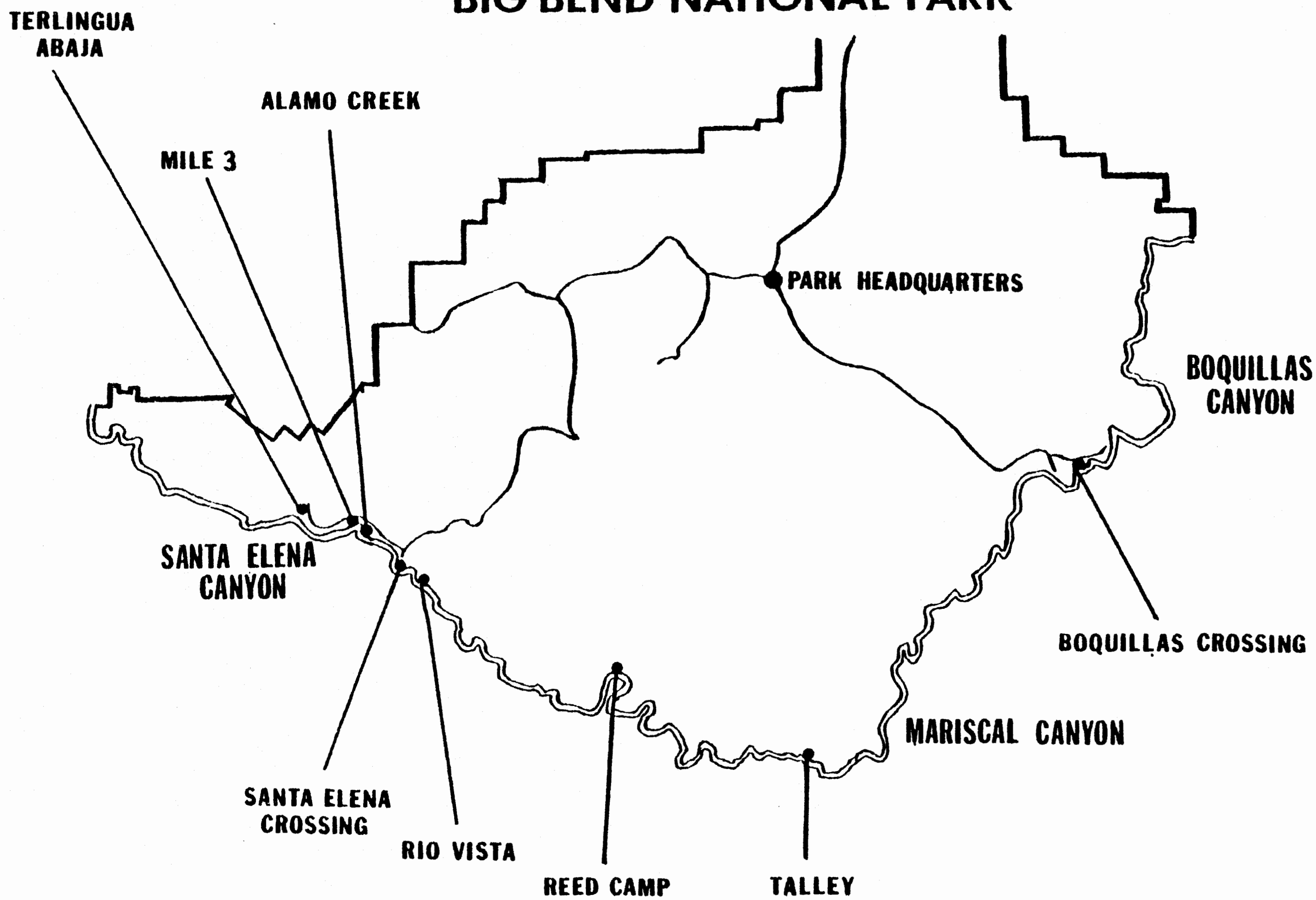
One site with native cottonwoods is approximately 6.5 km upstream from the mouth of Terlingua Creek near the ruins of Terlingua Abaja. Locations more distant from the Rio Grande were not investigated. The other 7 sites are on the Rio Grande floodplain. Four of the 7 sites are located on the first 16 km of river downstream from the mouth of Santa Elena Canyon and include the ones at Mile 3, Alamo Creek, Santa Elena Crossing, and Rio Vista. The remaining 3 sites are at Reed Camp, the west end of Mariscal Canyon at Talley Crossing, and near Boquillas Crossing.

Taxonomy

Native cottonwoods at all 8 sites were identified as Fremont cottonwood (*P. fremontii* subsp. *mesetae*) by use of the key developed by Eckenwalder (1977). Leaf and twig characteristics of the cottonwoods varied within and among sites. The variation patterns were probably the result of hybridization between *P. deltoides* subsp. *wislizenii* and *P. fremontii* subsp. *mesetae* (Eckenwalder 1977).

Fig. 4. Locations of 8 native cottonwood stands on the United States floodplain adjacent to the Rio Grande, Big Bend National Park, Texas.

COTTONWOOD STANDS ON THE RIO GRANDE IN BIG BEND NATIONAL PARK



Stand Characteristics

The number of cottonwood trees at the 8 sites ranged from 2 at Talley to > 100 at Santa Elena Crossing. Ten or fewer trees grew at 4 of the 8 sites. The total number of cottonwoods estimated to exist on the floodplain in the Park was 232.

Height, age, and dbh of undamaged and damaged cottonwoods indicated that the trees were moderately old. Seventy-seven percent of the cottonwoods at 4 sites (Mile 3, Alamo Creek, Santa Elena Crossing, and Rio Vista) were between 5.0 and 14.9 m tall (Fig. 5), 67 percent were 20-59 years old (Fig. 6), and 81 percent were 0.0-0.6 m dbh (Fig. 7). The largest tree recorded was 1.114 m dbh, 16.5 m tall, and 84 years old. The tallest tree was 17.7 m, the oldest 117 years. The shortest measured distance to the river for any cottonwood tree was 56 m at the Alamo Creek site. Fifty-five (48.2%) of the 114 cottonwood trees at the 4 sites were > 200 m from the river.

Irregularly formed trees, whose shapes had been influenced by environmental factors, such as flooding, were noted, especially at the Santa Elena Crossing site. A positive correlation ($r = 0.740$) existed between height and dbh of cottonwood trees at the 4 sites.

Cottonwoods at the Mile 3, Alamo Creek, Santa Elena Crossing, Reed Camp, and Talley sites grew in fine, sandy soils. These soils were dry and only occasionally saturated during extreme rises in river level. Cottonwoods at Terlingua Abaja and Boquillas Crossing grew in more moist conditions. Many of the trees at Terlingua Abaja grew in the gravel creekbed of Terlingua Creek, while trees at Boquillas Crossing grew in a spring-fed swamp.

Cottonwood trees were widely distributed throughout the Alamo

Fig. 5. Height distribution of native cottonwood trees at 4 sites, Big Bend National Park, Texas, 1980-1981.

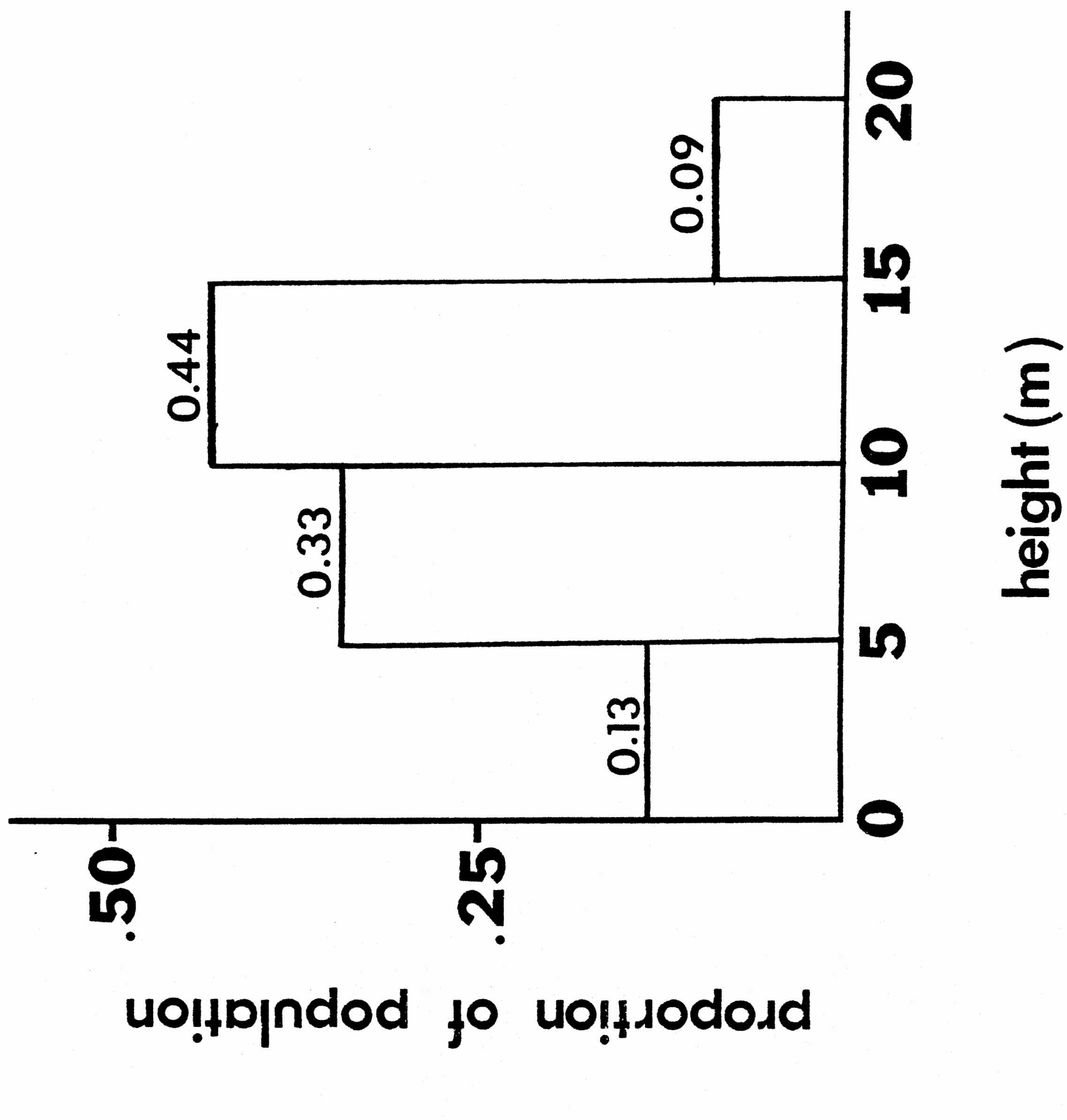

0.13
0.33
0.44
0.09
0
5
10
15
20
height (m)
.50
.25
proportion of population

Fig. 6. Age structure of native cottonwood trees at 4 sites, Big Bend National Park, Texas, 1980-1981.

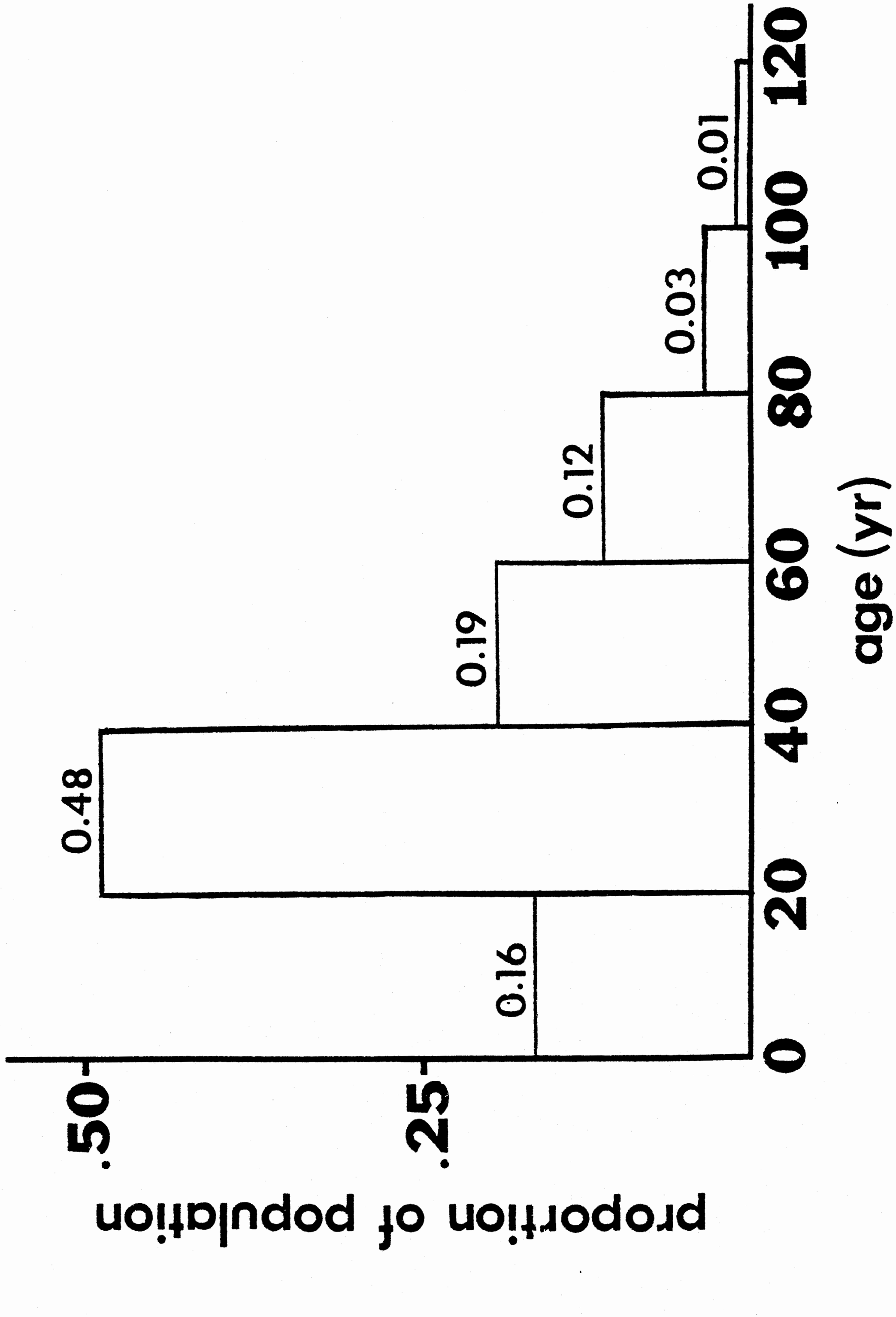
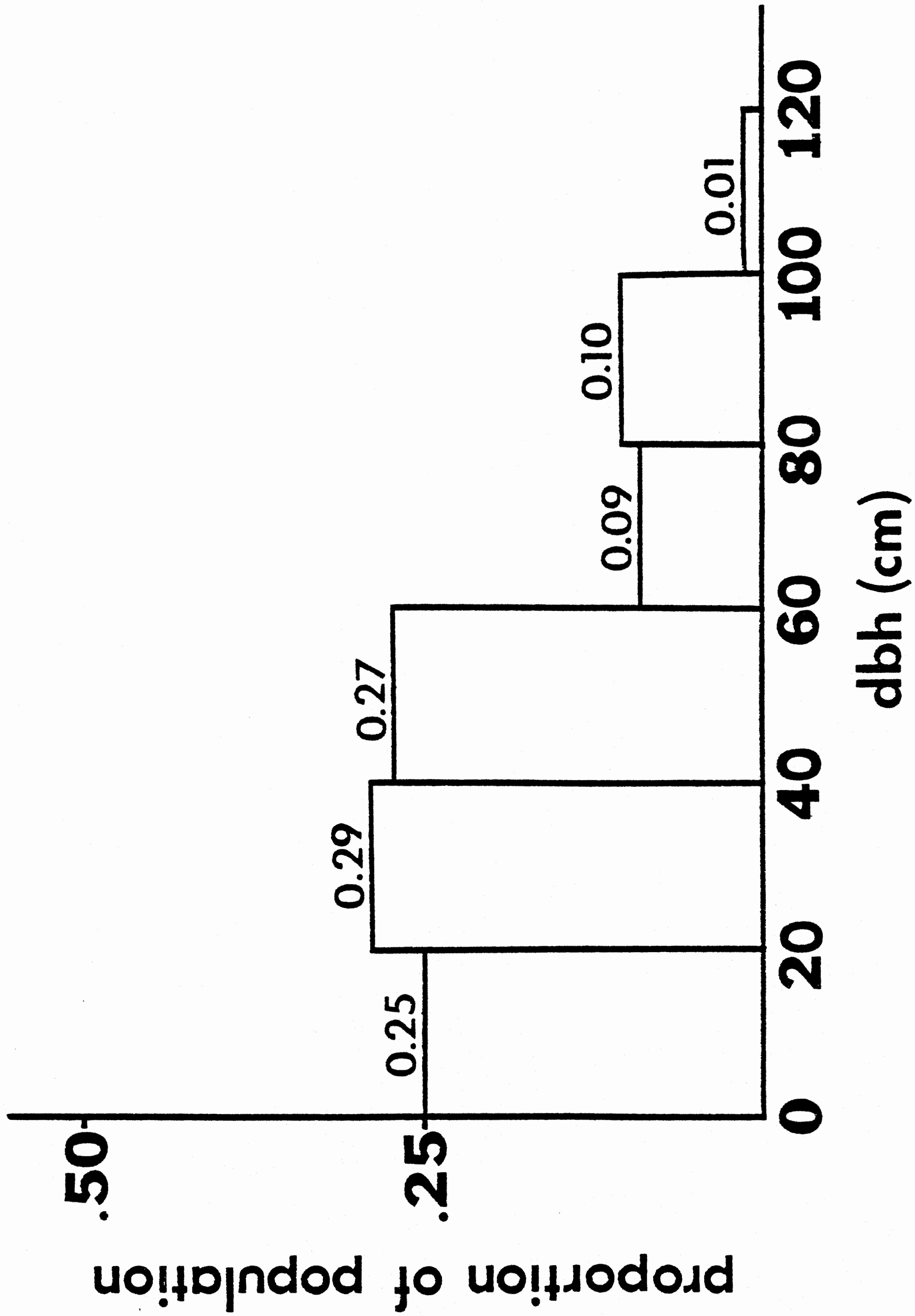

proportion of population
.50
.25
0
20
40
60
80
100
120
age (yr)
0.16
0.48
0.19
0.12
0.03
0.01

Fig. 7. Distribution of native cottonwood trees by diameter class at 4 sites, Big Bend National Park, Texas, 1980-1981.


proportion of population
.50
.25
dbh (cm)
0
20
40
60
80
100
120
0.25
0.29
0.27
0.09
0.10
0.01

Creek, Santa Elena Crossing, and Rio Vista sites. Many solitary trees occurred at these sites. Cottonwood trees grew in one clump at the Mile 3, Reed Camp, Talley, and Boquillas Crossing sites. Most cottonwoods at Terlingua Abaja grew in a dense stand, however, solitary trees were scattered throughout the site.

Reproduction and Regeneration

Native cottonwood seedlings grew at Terlingua Abaja. Seedlings were not found anywhere else on the study area. Regenerative shoots were found at all sites and were quantified at Mile 3, Alamo Creek, Santa Elena Crossing, and Rio Vista (Table 1). Root sprouting was uncommon, occurring on only 10.5% of all trees with regenerative structures and on 7.0% of all trees examined. Epicormic shoots occurred on all trees with regenerative structures and on 66.7% of all trees examined. The average number of epicormic shoots/tree was greater than the average number of root sprouts/tree for both damaged and undamaged trees. Damaged trees had more total shoots than undamaged trees. Damaged trees had 0.7 root sprouts/tree vs. 0.1 for undamaged trees. Root sprouts did not occur more than 3 m from a parent stem and there were no large clumps of root sprouts at any of the sites.

Disturbance Factors

Evaluation of relative amounts of human and livestock disturbances and tamarisk invasion at the 8 native cottonwood sites indicated that human disturbance was usually low and was moderate at only 3 sites. Livestock disturbance was moderate at 5 sites and high only at Santa Elena Crossing. Tamarisk invasion was moderate at 5 sites and high at Mile 3. No sites had high values for more than 1 disturbance factor, however, one site, Terlingua Abaja, had low values for all disturbance

Table 1. Regeneration by root sprout and epicormic shoot growth for damaged and undamaged cottonwood trees in 4 native stands on the Rio Grande floodplain, Big Bend National Park, Texas, 1980-1981.

	Trees with root sprouts				Trees with epicormic shoots				Total # trees with reproduction				$\bar{X}$ root sprouts/tree		$\bar{X}$ epicormic shoots/tree	
	damaged		undamaged		damaged		undamaged		damaged		undamaged		damaged	undamaged	damaged	undamaged
Cottonwood stand	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%				
Mile 3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Alamo Creek	0	0.0	2	100.0	1	4.8	20	95.2	1	4.8	20	95.2	0.0	0.2	12.0	4.0
Santa Elena Crossing	3	60.0	2	40.0	10	26.3	28	73.7	10	26.3	28	73.7	1.1	0.1	11.9	5.9
Rio Vista	1	100.0	0	0.0	12	70.6	5	29.4	12	70.6	5	29.4	0.2	0.0	17.4	5.2
Total	4	50.0	4	50.0	23	30.3	53	69.7	23	30.3	53	69.7	0.7	0.1	13.8	4.3

factors (Table 2).

Willow Resources

Locations

Willows grew at 32 sites on the United States floodplain along the Rio Grande in the Park (Fig. 8). Eight sites (25.0%) had high densities of willows, the density at 13 (40.6%) sites was intermediate, and 11 (34.4%) sites had low densities. The largest concentrations of willows were adjacent to the first 5 km of river downstream from the mouth of Santa Elena Canyon, the 10 km of river between Johnson Ranch and Reed Camp, the 5 km of river upstream from the entrance of Mariscal Canyon, and throughout Rio Grande Village from Daniel's Ranch to the Nature Trail. Very few or no small willows grew in the 5 river canyons in the Park. Willows were scarce on the Mexican floodplain. Willow readily colonizes silt deposits and exposed gravelbars at the river's edge, but is often in competition with baccharis, tamarisk, and common and giant reed. Willow, a shade intolerant species, is often an unsuccessful competitor if shaded by faster growing plants.

Taxonomy

Four species of willow grow along the Rio Grande in the Park; black willow (*S. nigra*), sandbar willow (*S. interior*), Goodding willow (*S. gooddingii*), and yew willow (*S. taxifolia*) (McDougall and Sperry 1951). Of these, black and sandbar willow were most common on the study area.

Stand Composition

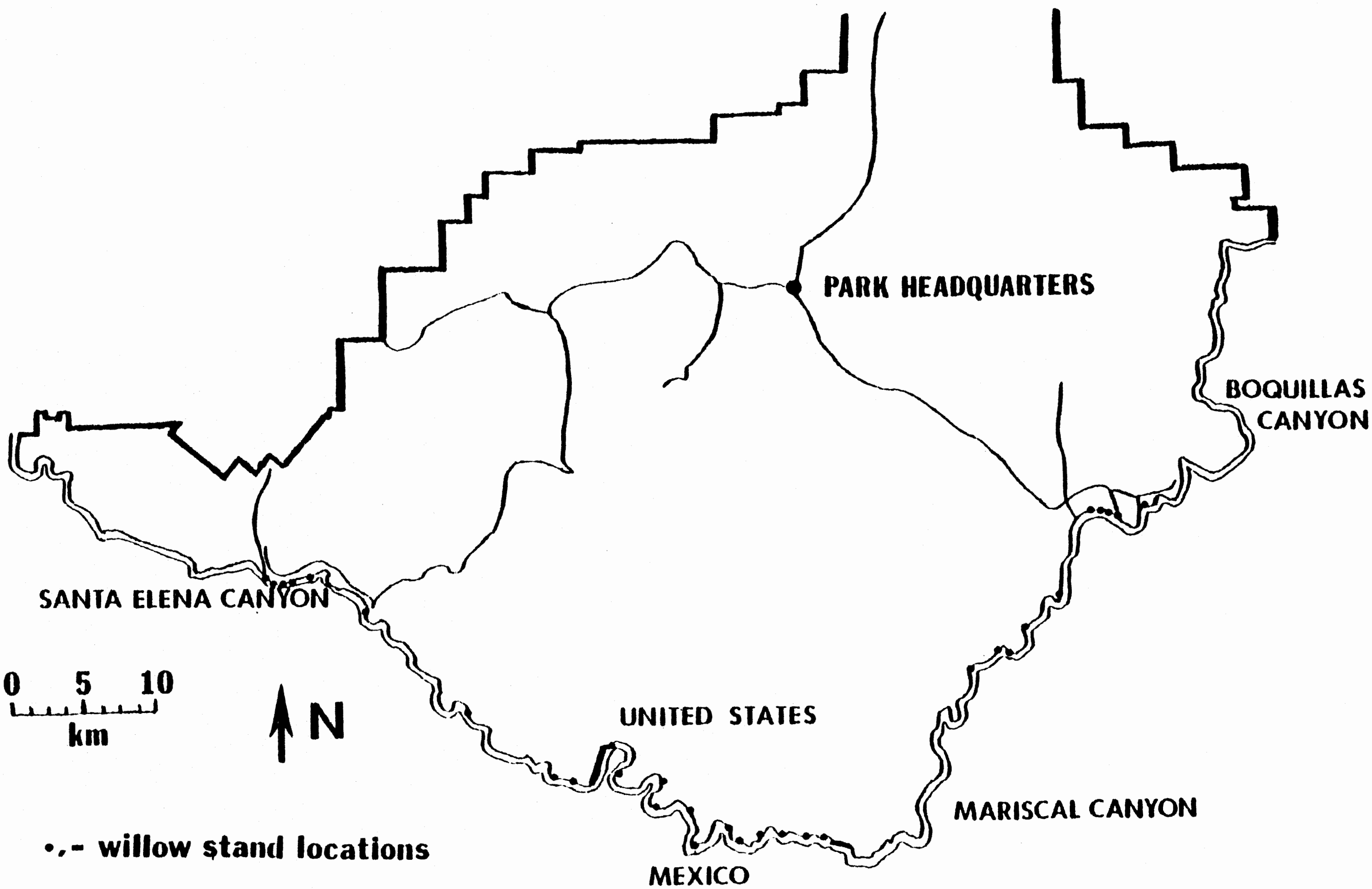
Three high density willow stands in Rio Grande Village were sampled to determine composition by species and diameter class. Some trees in all of the stands had been felled by beaver previous to the

Table 2. Disturbance factors at native cottonwood stands on the Rio Grande floodplain, Big Bend National Park, Texas, 1980-1981.

Site	Human disturbance	Tamarisk invasion	Livestock disturbance	Beaver activity during study
Terlingua Abaja	low	low	low	yes
Mile 3	low	high	moderate	no
Alamo Creek	low	moderate	moderate	no
Santa Elena Crossing	moderate	moderate	high	yes
Rio Vista	moderate	moderate	moderate	yes
Reed Camp	low	moderate	moderate	no
Talley	moderate	moderate	moderate	no
Boquillas Crossing	moderate	low	low	no

Fig. 8. Locations of 32 willow stands on the United States floodplain adjacent to the Río Grande, Big Bend National Park, Texas, 1980-1981.

BIG BEND NATIONAL PARK



study. Beaver were not active in the stands during sampling, but felled trees were found in each stand later in the study. One stand abutted the river, one was 7 m from the river, and one was 35 m from the river behind a large gravelbar. The stands were approximately rectangular, the long sides parallel to the river. Areas of stands were 0.150, 0.126, and 0.375 ha. The gravelbars between the trees and the river in stands 1 and 3 were associated with bends in the river. As a result, willows at the front corners of the stands were closer to the river than other trees along the front edges. At stands 1 and 3 the majority of seedlings was located at the front corners closest to the river. At stand 2 seedlings appeared evenly distributed along the front edge of the stand. Small trees and seedlings were most dense on the river side of the stands where sunlight and water were most abundant. Few seedlings grew in the interior of the stands. Within each stand average diameter of trees increased and density decreased as distance from the river increased. Baccharis and tamarisk trees grew in the stands, most commonly along the front edges.

Sampling results are presented in Table 3. Baccharis and tamarisk trees made up 54.3% of stand 1, 38.9% of stand 2, and 45.6% of stand 3. However, 88.6% of all tamarisk and baccharis trees were < 2.54 cm dbh. Of trees > 2.53 cm dbh, 75.4% were willow. Willow trees < 1.26 cm dbh made up 68.4%, 69.2%, and 16.3% of the respective samples. In stands 1 and 2 trees < 5.08 cm made up 99.2% of the samples, respectively. In stand 3, 81.4% of the trees had diameters < 5.08 cm. No trees > 15 cm dbh grew in the willow stands, however, several large willows grew farther from the river behind the stands. These trees were not included in the sampled areas because they were not within the

Table 3. Composition of 3 high density willow stands by 1.26-cm diameter classes, Big Bend National Park, Texas, 1980-1981.

Stand	Number of willow trees	Tree diameter classes (cm) 0.00-1.26	1.27-2.53	2.54-3.80	3.81-5.07	5.08-6.34	6.35-7.61	7.62-10.16	10.17-12.69
1	354	242 (68.4)	79 (22.3)	25 (7.1)	5 (1.4)	1 (0.3)	1 (0.3)	3 (0.3)	0 (0.0)
2	380	263 (69.2)	47 (12.4)	29 (7.6)	16 (4.2)	8 (2.1)	6 (1.6)	6 (1.6)	5 (1.3)
3	655	107 (16.3)	228 (34.8)	117 (17.9)	81 (12.4)	49 (7.5)	28 (4.3)	31 (4.7)	14 (2.1)

boundaries of continuous willow growth. Generally, large trees were separated from the rest of the stand by dense growth of tamarisk, baccharis, and common reed.

Willow stands assigned intermediate and low density values were composed of greater proportions of tamarisk, baccharis, and common reed and had smaller areas of continuous willow growth than high density stands. Fewer large willows (> 15 cm) were present and stands of seedlings were rare.

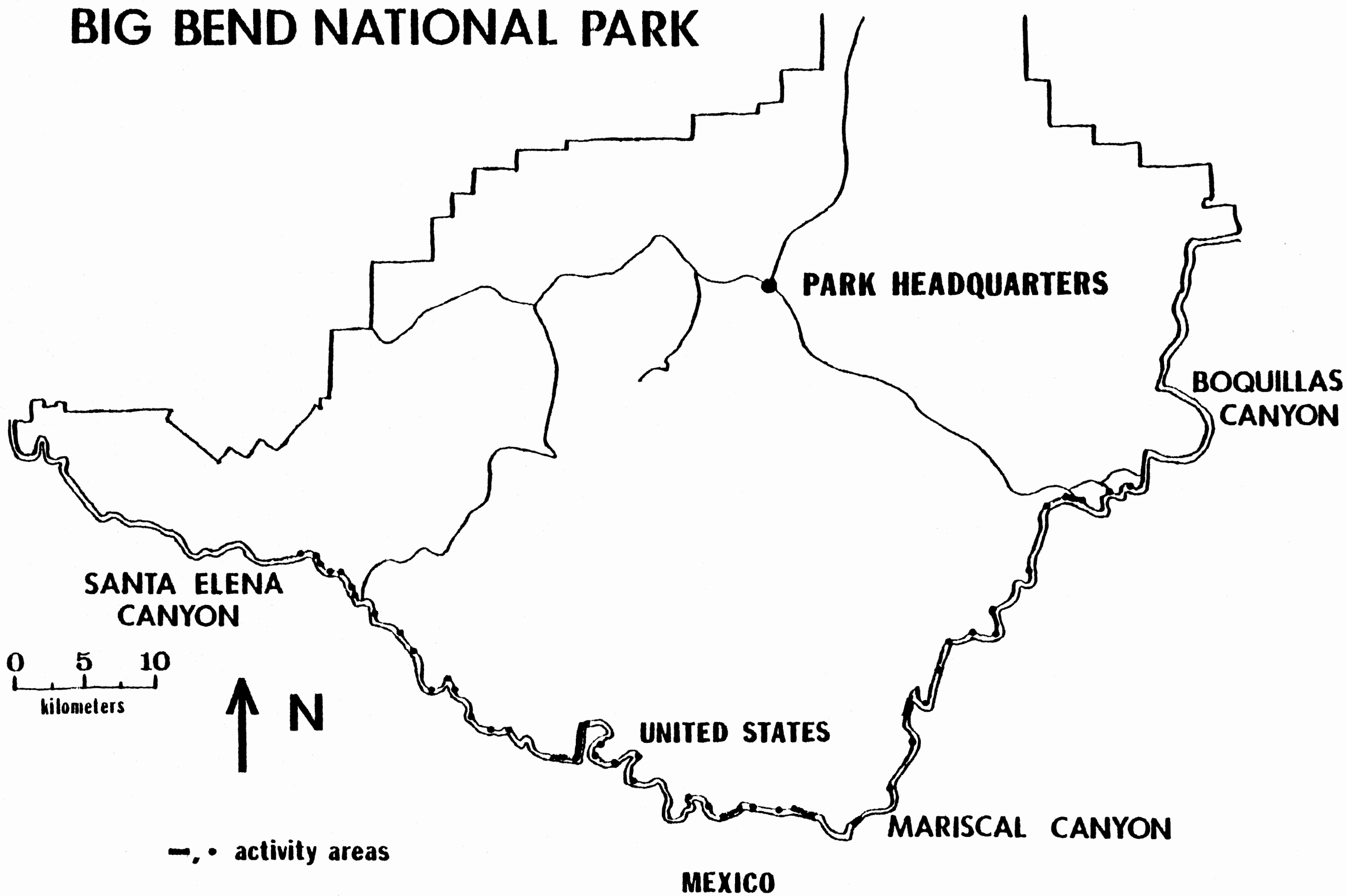
Mexican Beaver

Areas of Activity

Forty-three distinct areas of beaver activity were delineated on 131 km of the Rio Grande between the mouth of Santa Elena Canyon and the west end of Boquillas Canyon (Fig. 9). These areas totaled 62.9 km (48.5%) of the study area. An area of beaver activity was defined as a distance along the riverbank used by a specific group of beaver for feeding, scent mount deposition, den site excavation, and other activities. When an area was occupied by 1 colony, an activity area was equivalent to home range as defined by Dasmann (1964, p. 117). However, 1 activity area was not always equivalent to 1 colony. Colony boundaries were difficult to determine, especially where activity was continuous over a long stretch of river. One 8-km stretch of river showed continuous use along its length and was considered 1 activity area because colony boundaries could not be determined. I estimated 54 colonies occupied the activity areas based on the amount of feeding activity and mean size of recognizable beaver colonies.

Beaver occupied various river habitats along the Rio Grande. Thirty-seven (86.0%) activity areas were adjacent to broad, flat

Fig. 9. Locations of 43 areas of beaver activity along the Rio Grande between the mouth of Santa Elena Canyon and the west end of Boquillas Canyon, Big Bend National Park, Texas, 1980-1981.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floodplain. Six (14.0%) were found in 4 of 5 river canyons; 3 in 2 major canyons, and 3 in the 2 smaller canyons. One major canyon, Boquillas, had no beaver activity even though there were areas where floodplain vegetation grew on large open siltbars. Areas of beaver activity were often adjacent to wide parts of the floodplain where stands of woody vegetation were present. Mixed stands of willow, tamarisk, and baccharis grew adjacent to areas of exposed silt and gravel at the river's edge and were common. Dense stands of common and giant reeds lined much of the riverbank in these areas where rocky slopes rose from the riverbank. Vegetation on the Mexican floodplain had been severely modified by human use and livestock grazing, and as a result, few sites on the Mexican floodplain showed any indication of beaver activity.

Activity areas in canyons were near siltbars with woody vegetation. Siltbars were uncommon in the canyons. Tamarisk, white-thorned acacia (<u>Acacia constricta</u>), and baccharis were most common as small trees or seedlings.

One activity area in Mariscal Canyon was 3 km long and was inhabited by 2 beaver. The boundaries of the colony were marked by scent mounds on small siltbars. Throughout most of the canyon, sheer walls and steep, rocky slopes bordered the river, leaving little room for plant growth. Feeding sites were scattered throughout the colony, but centered at 2 sites where siltbars with abundant vegetation existed.

Another colony of beaver occupied unusual habitat along a section of Terlingua Creek approximately 6.5 km upstream from its confluence with the Rio Grande. Most of the streamflow along this section was restricted to a channel < 2 m wide and < 10 cm deep over the gravel bottom of the much wider, dry creekbed. Depressions in the creekbed allowed water to collect in several pools up to 1.25 m deep. The creek became dry 8.5 km upstream from its mouth. Willow, baccharis, and cottonwood grew at few places in and along the sides of the creek. One small pool supported cattail (*Typha latifolia*) growth. Beaver occupied this area during Spring 1981. No new activity was seen after March. Beaver may have moved into this area during or after flooding which filled the creek for short periods of time in October, February, and March. This area of beaver activity appeared very similar to an area occupied by beaver in Arizona. Ffolliot et al. (1976) described a semi-arid region in Arizona where beaver inhabited a creek with intermittent streamflow that had several isolated pools and was 14.5 km from the nearest perennial water.

Population Estimate

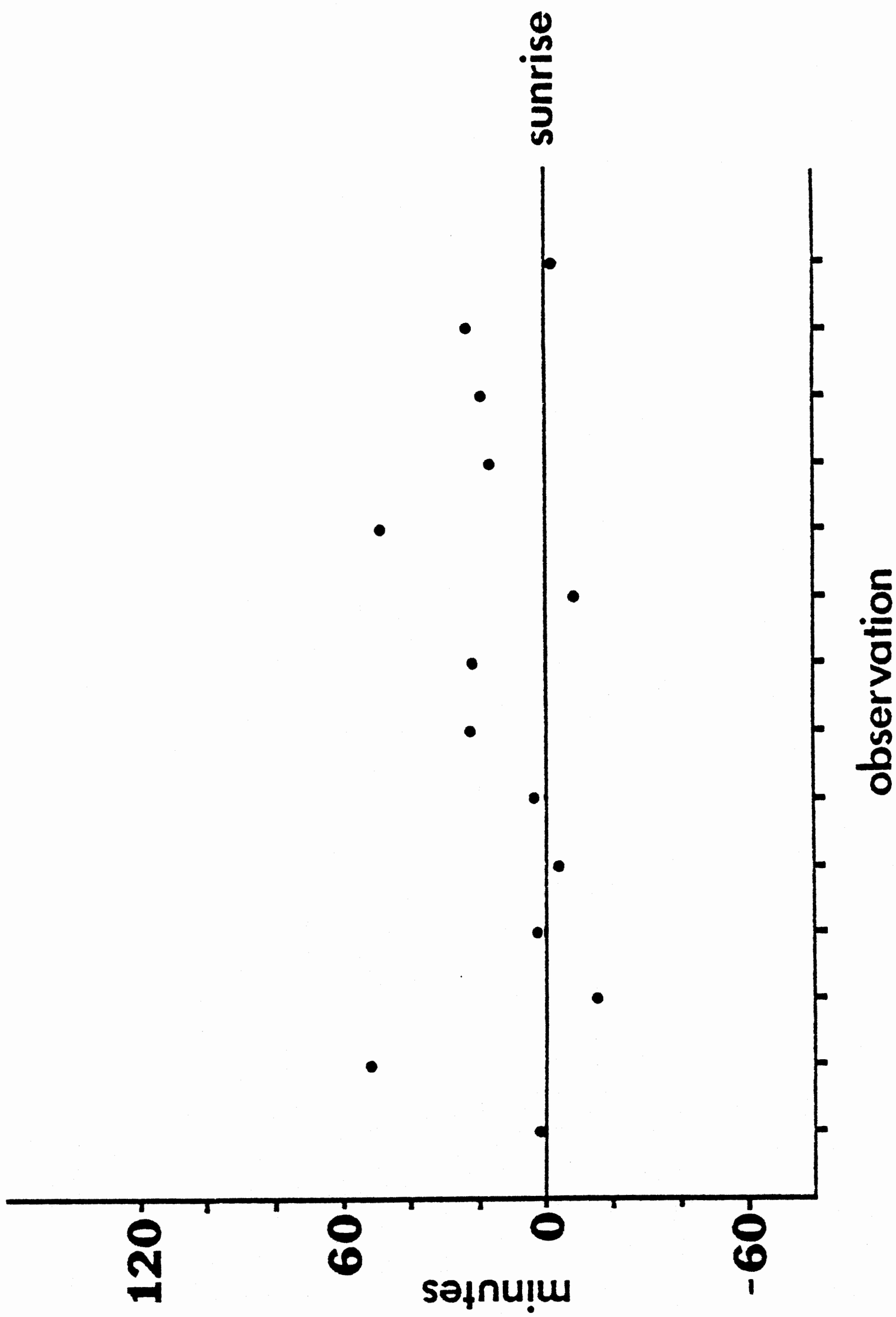
Seventy-three observations involving 100 beaver were made over 12 months. The mean number of beaver seen per observation was 1.39 ± 0.76. Fifty-three (72.6%) observations were of 1 beaver, 11 (15.1%) were of 2 beaver, and 6 (8.2%) were of 3 beaver. The maximum number of beaver seen at 1 time was 4 [observed twice (2.7%)] . One observation was of an undetermined number of beaver.

Twenty-three (31.5%) observations were of beaver flushed from resting places along the riverbank. Flushed beaver were usually observed for < 1 min. Observations of beaver flushed from resting sites were made 98 min. after sunrise to just before sunset. Fifty (68.5%) observations were made during hours of activity. The earliest recorded activity began 45 min. after sundown and the latest ended 4 hr. 52 min. after sunrise. Observations of beaver conducted from several hours before sunrise to the end of the activity period revealed that most activity ended within 1 hr. after sunrise (Fig. 10).

Thirty-one individual beaver were seen during the study period, 17 of which comprised 5 colonies. Four beaver occupied a site 1.6 km downstream from the mouth of Santa Elena Canyon, 3 lived in a colony 3.6 km downstream from the mouth of the Canyon, 2 inhabited a site in Hot Springs Canyon, 3 occupied a colony near the Pumphouse in Rio Grande Village, and 5 inhabited a colony site on the island downstream from Boquillas Crossing. The remainder were seen along various stretches of the river where exact counts of colony sizes were not made.

Huey (1956) recommended that habitat type be considered a factor in estimates of beaver populations in New Mexico. I assumed that high habitat quality was correlated with high beaver density. I then compared the number of beaver in each activity area with habitat quality and expanded the relationship for the entire study area. An estimate of 134 beaver was made for 131 km of the Rio Grande between the mouth of Santa Elena Canyon and the west end of Boquillas Canyon, an overall density of 1.02 beaver/km. The estimate does not include beaver inhabiting Santa Elena or Boquillas Canyons or Terlingua Creek. Approximately 70 percent of the known population inhabits the stretch of river between Santa Elena and Mariscal Canyons. Connor and Feeley (unpubl. rep.) estimated 94 beaver for 113 km of river bordering the Park, a density of 0.83 beaver/km. Huey (1956) estimated 0.77 beaver/km for 720 km of the Rio Grande in New Mexico. Based on the estimate of 54 colonies there is an average of 2.48 beaver/colony. Bradt (1938) found an average of 5.1 beaver/colony in Michigan. Connor and Feeley (unpubl. rep., p. 12) estimated "... approximately two per colony..."

Fig. 10. Times of cessation of beaver activity, Big Bend National Park, Texas, 1980-1981.


sunrise
observation
minutes
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for Big Bend National Park.

I estimated 10 beaver inhabited 21.5 km of river in Mariscal, San Vicente, and Hot Springs Canyons, a density of 0.47 beaver/km. One hundred twenty-four beaver occupied 109.5 km of river exclusive of canyons, a density of 1.13 beaver/km. Beaver densities in canyons were not equal to densities on sections of river outside canyons (Chi-square, $0.01 > P > 0.005$).

Greatest estimated densities of beaver in the Park were along the first 4 km of river downstream from the mouth of Santa Elena Canyon (3.25 beaver/km), the 7.2 km of river from Johnson Ranch to Reed Camp (2.08 beaver/km), and near Talley (2.00 beaver/km). Connor and Feeley (unpubl. rep.) reported the most concentrated area of beaver activity was near Johnson Ranch.

Beaver Use of the Resources

Cottonwood Damage

At least 29 (12.5%) of the estimated 232 native cottonwoods along the river were damaged by beaver. Of the 29 damaged trees, 15 (51.7%) were felled, 5 (17.2%) were deeply chewed, the cambium on 2 (6.9%) was girdled, 2 (6.9%) were lightly chewed, and some branches on 5 (17.2%) trees were removed (Table 4).

The Rio Vista site was most heavily used by beaver. At least 12 cottonwoods were damaged. The trees were 68 to > 200 m from the river. The lack of other food sources in the area may have influenced heavy use of the site. The Rio Vista site was within the boundaries of a beaver colony during the study period. The stand at Santa Elena Crossing was more distant from beaver colonies and was used by beaver for only short periods. Although beaver had damaged trees at the Mile 3 and

Table 4. Beaver damage to cottonwoods at 8 sites on the Rio Grande floodplain, Big Bend National Park, Texas, 1980-1981.

Cottonwood stand	No. trees	No. trees examined	No. trees damaged	Felled	Deep chewing	Cambium girdling	Slight chewing	Felled branches
Mile 3	8	8	1	0	1	0	0	0
Alamo Creek	36	36	1	1	0	0	0	0
Santa Elena Crossing	100[a]	52	15	5	3	1	1	5
Rio Vista	30[a]	18	12	9	1	1	1	0
Reed Camp	6	6	0	0	0	0	0	0
Boquillas Crossing	10	10	0	0	0	0	0	0
Talley	2	2	0	0	0	0	0	0
Terlingua Abaja	40[a]	*	*	*	*	*	*	*
Total	232[a]	122	29	15	5	2	2	5

[a] estimated total; no exact count of trees in the stand was made

* trees were damaged by beaver, but no exact count was made

Alamo Creek sites, no new damage was noted during the field season. No damage was evident at Reed Camp, Talley, and Boquillas Crossing sites, although beaver were active near all the sites. Beaver were active at Terlingua Abaja, where sufficient water was present, felling small cottonwoods growing in the creekbed. Large trees distant from the creekbed were not damaged.

Distance of trees from the river influenced beaver use. Damaged trees were much closer to the river than undamaged trees. At Rio Vista 12 of the 14 trees closest to the river were damaged by beaver. At Alamo Creek the 1 damaged tree was the second closest to the river. At Santa Elena Crossing the 15 damaged trees were among the 22 closest trees to the river. The greatest distance from the river that beaver traveled to cut cottonwood trees was 120 m. Some damaged cottonwoods were > 200 m from the river, but damage was not recent and the actual distance from the river at the time of damage could not be determined. Hiner (1938) recorded a maximum distance of 138 m traveled by beaver to cut trees.

The relationship between dbh of cottonwood trees and damage by beaver was analyzed. Table 5 shows the number of damaged vs. undamaged cottonwood trees in 0.1-m diameter class increments at 4 sites. A Chi-square test of significance (Snedecor and Cochran 1967) tested the null hypothesis that cottonwood trees were damaged by beaver in equal proportion to their availability in the diameter classes. The null hypothesis was rejected at the 5 percent level ($0.0025 > p > 0.01$). Beaver appeared to prefer smaller diameter trees, although some large trees close to the river were damaged. These results suggest that distance from the river and tree diameter were important factors

Table 5. Number of damaged and undamaged cottonwood trees in 0.1-m diameter classes in 4 cottonwood stands, Big Bend National Park, Texas, 1980-1981.

	Upper limit of 0.1-m dbh interval												
	0.09	0.19	0.29	0.39	0.49	0.59	0.69	0.79	0.89	0.99	1.09	1.19	Total
Undamaged trees	4	9	14	15	12	17	4	3	5	2	0	0	85
	(4.7)	(10.6)	(16.5)	(17.6)	(14.1)	(20.0)	(4.7)	(3.5)	(5.9)	(2.4)	(0.0)	(0.0)	(100.0)
Damaged trees	8	7	3	1	2	0	2	1	2	2	0	1	29
	(27.6)	(24.1)	(10.3)	(3.4)	(6.9)	(0.0)	(6.9)	(3.4)	(6.9)	(6.9)	(0.0)	(3.4)	(99.8)
All trees	12	16	17	16	14	17	6	4	7	4	0	1	114
	(10.5)	(14.0)	(14.9)	(14.0)	(12.3)	(14.9)	(5.3)	(3.5)	(6.1)	(3.5)	(0.0)	(0.9)	(99.9)

determining beaver use of cottonwoods.

Beaver were active at cottonwood sites exhibiting low and moderate levels of human disturbance and tamarisk invasion and low, moderate, and high levels of livestock disturbance (Table 2). Beaver were active at Rio Vista and Santa Elena Crossing where human disturbance was moderate. Livestock disturbance at these sites was infrequent and of short duration and human activity occurred primarily during daylight hours. Beaver use of these areas was not constant throughout the study period and tended to coincide with absence of livestock. Cottonwood trees in Mexico opposite the Santa Elena Crossing site were not used by beaver, presumably due to the high levels of human and livestock use. Beaver were active at 2 sites where tamarisk invasion was moderate and 1 site where it was low. No recent sign of beaver activity was noted at Mile 3 where there was a high level of tamarisk invasion.

The 5 sites with native cottonwoods that did not receive beaver use had various levels of disturbance with most values low or moderate. Active beaver colonies existed near 3 of the sites, but beaver did not damage cottonwoods. High densities of willow and baccharis closer to the river at these sites may have inhibited beaver use of the cottonwoods. A scarcity of food probably discouraged beaver from inhabiting the Alamo Creek and Mile 3 sites.

Use of Willows

Beaver used willow extensively and were active in 26 (81%) of 32 willow stands on the U.S. floodplain. Of 6 stands where beaver were not active, 4 had low densities of willow, 1 was intermediate, and 1 had high density. The 1 stand with high willow density was near an area of high human use at a heavily traveled border crossing near the

Mexican town of San Vicente. A more comprehensive account of willow use by beaver is presented in the analysis of food habits.

Food Habits

At least 19 species of plants were cut by beaver during the study period. Fifteen (78.9%) species were trees or shrubs. Beaver did not construct dams or lodges and I assumed that all tree felling was related to feeding. The most common foods of beaver in the Park were willow, baccharis, and tamarisk.

Beaver ate 4 species of herbaceous plants. One species of sedge (*Cyperus laevitagus*) was eaten. Beaver dug silt from the base of the stems to expose the roots which were consumed. Common and giant reed were the most commonly consumed herbaceous plants and appeared to make up the bulk of the diet for certain colonies for short periods of time. Beaver ate the roots and leaves of the reeds. Cattail was localized and uncommon on the banks of the Rio Grande. The greatest concentrations grew in spring-fed swamps adjacent to the river. Cattail roots were eaten by beaver during the summer months.

Woody species made up the majority of plants cut by beaver. The limited number of cottonwoods along the river restricted its use. Willow was the major food item at 20 of 27 willow stands where beaver were active. At least 2 species of baccharis were consumed. No distinction between species was made when collecting food data, but it appeared that seepwillow baccharis (*B. glutinosa*) was most commonly available and used. Tamarisk was eaten throughout the study area although it appeared to be the major food item at only 3 colonies. Most feeding activity on tamarisk was in mixed stands of tamarisk, baccharis, willow, and common reed. There was no evidence of feeding activity in dense tamarisk bosques.

Other woody species were eaten less frequently. White-thorned acacia was consumed by beaver in 3 colonies and was the major food item in 2. In Mariscal Canyon, where other foods were scarce, beaver concentrated their activity around 2 clumps of acacia. Beaver in a colony near Boquillas Crossing consumed acacia from January to early March 1981. Fragrant ash (Fraxinus cuspidata), burrobrush (Hymenoclea monogyra), and Mormon tea (Ephedra torreyana) were cut by beaver at several sites, but were not major food items. Desert willow (Chilopsis linearis) and common mesquite were cut infrequently. Use of wild tobacco tree (Nicotiana glauca) was recorded once. Stem use was not determined, but it appeared that it had been cut incidentally along a runway leading to a heavily used willow stand.

No distinct seasonal food pattern was noted. However, use of herbaceous vegetation was greatest during summer months. No evidence of beaver use of cattail or sedge was seen in the fall or winter. Woody species were consumed at all times of the year, but appeared most heavily used in fall and winter. Baccharis was cut throughout the year, but was cut least frequently in the spring.

Food habits in 5 beaver colonies were investigated to document food habits within individual colonies. The colonies were located at the mouth of Santa Elena Canyon (SEC), 1.6 km downstream from the mouth of Santa Elena Canyon (SER), in Hot Springs Canyon (HSP), at the Pumphouse in Rio Grande Village (PUM), and near the Research Station at Boquillas Crossing (RES). Seven species of woody vegetation were felled by beaver in the 5 colonies. Willow was felled most often in 3, tamarisk in 1, and baccharis in 1. Desert willow, burrobrush, and tobacco tree made up a small proportion of the felled trees and acacia was felled in only 1 colony. Willow, baccharis, and tamarisk were all available in 4 of 5 colonies, and in 3, willow was felled most often. Baccharis was taken most often in the remaining colony with all 3 species, and tamarisk was felled most often in the colony where willow was absent and baccharis was scarce (Table 6). In colonies where these 3 food items were absent or scarce, other foods, such as acacia and common reed, were used.

The mean diameter for all trees felled in the 5 colonies was 1.63 cm (Table 7). Beaver felled trees 0.2-10.6 cm diameter at stump height. Of the 3 most commonly felled species, tamarisk had the smallest mean diameters for all colonies, willows had the largest, and baccharis was intermediate.

The mean distance from the river traveled by beaver to fell trees in the 5 colonies was 15.07 m. The extremes were 0.00 and 74.50 m. There was a great deal of variation in mean distances traveled among colonies (Table 8). Beaver at the PUM and RES colonies traveled the shortest distances presumably because of an abundance of desirable food near the river. Beaver at the HSP, SEC, and SER colonies often crossed wide gravelbars to obtain food, and thus, traveled greater mean distances from the river.

Based on mean diameter values for each species, it was expected that the mean distance traveled by beaver in each colony to fell trees would vary among species. Acacia, desert willow, burrobrush, and wild tobacco tree were not included in this analysis. Tamarisk trees had the smallest mean diameters and were expected to have the smallest mean distance traveled values. The largest value was expected for

Table 6. Percentages of trees felled within colonies for 5 beaver colonies along the Rio Grande, Big Bend National Park, Texas, 1980-1981.

	Beaver Colony				
Tree species	HSP[1]	PUM[2]	RES[3]	SEC[4]	SER[5]
Acacia	0.00	0.00	5.97	0.00	0.00
Baccharis	11.52	25.81	81.88	9.87	12.20
Desert willow	0.85	0.00	0.00	0.00	0.00
Burrobrush	2.13	0.16	0.00	4.29	0.00
Wild tabacco tree	0.00	0.00	0.00	0.00	0.07
Willow	0.00	59.71	0.00	82.45	81.29
Tamarisk	85.50	14.32	12.15	3.39	6.44
Total	100.00	100.00	100.00	100.00	100.00

[1] Hot Springs colony located in Hot Springs Canyon.

[2] Pumphouse colony located in Rio Grande Village.

[3] Research Station colony located at Boquillas Crossing.

[4] Santa Elena Canyon colony located at the mouth of Santa Elena Canyon.

[5] Santa Elena Roadside colony located 1.6 km downstream from the mouth of Santa Elena Canyon.

Table 7. Mean diameter (cm) of trees felled by beaver in 5 colonies in Big Bend National Park, Texas, 1980-1981.

	Beaver colony					
Tree species	HSP[1]	PUM[2]	RES[3]	SEC[4]	SER[5]	All colonies
Acacia			2.62			2.62
Baccharis	1.08	1.32	1.23	0.77	1.40	1.25
Desert willow	1.10					1.10
Burrobrush	1.03	1.25		0.79		1.07
Wild tobacco tree					1.50	1.50
Willow		2.23		1.69	2.01	1.98
Tamarisk	0.94	1.01	1.21	0.99	1.54	1.12
All trees	0.96	1.82	1.32	1.53	1.90	1.63

[1] Hot Springs colony located in Hot Springs Canyon.

[2] Pumphouse colony located in Rio Grande Village.

[3] Research Station Colony located at Boquillas Crossing.

[4] Santa Elena Canyon colony located at the mouth of Santa Elena Canyon.

[5] Santa Elena Roadside colony located 1.6 km downstream from the mouth of Santa Elena Canyon.

Table 8. Mean, minimum, and maximum distances (m) from the river traveled by beaver to fell trees in 5 colonies on the Rio Grande, Big Bend National Park, Texas, November 1980 - May 1981.

Colony	$\bar{X}$	Min.	Max.
HSP[1]	13.62	2.00	32.50
PUM[2]	5.46	0.30	29.00
RES[3]	6.09	0.00	23.00
SEC[4]	22.65	0.50	74.00
SER[5]	22.94	1.00	74.50
All colonies	15.07	0.00	74.50

[1] Hot Springs colony located in Hot Springs Canyon.

[2] Pumphouse colony located in Rio Grande Village.

[3] Research Station colony located at Boquillas Crossing.

[4] Santa Elena Canyon located at the mouth of Santa Elena Canyon.

[5] Santa Elena Roadside colony located 1.6 km downstream from the mouth of Santa Elena Canyon.

willow and an intermediate value for baccharis.

The expected trend was evident in 4 of 5 colonies (Table 9). At the RES colony beaver traveled a shorter mean distance from the river to fell baccharis trees than they did for tamarisk trees. The lack of tamarisk seedlings near the river at this site may partially explain the deviation from the expected trend.

I derived prediction equations for the dry weight of bark in grams on trees with known diameters for willow, baccharis, and tamarisk (Table 10). The equations are most useful within the range of data for each species, but were also used to estimate weights of bark on trees in larger diameter classes, since those trees made up only a small proportion of the total number of trees felled. Felled willow trees provided the greatest amount of available food in grams of dry bark in all 3 colonies where willow was felled. Felled tamarisk and baccharis trees provided the greatest amount each in 1 colony (Table 11).

Den Sites

Instead of building lodges, which are associated with lakes and areas of limited water flow, most beaver in the Rio Grande bottomlands live in burrows excavated in the soft alluvial soils of the riverbanks (Schmidly and Ditton 1976, Schmidly 1977, p. 95). Dams are generally not built or found along the Rio Grande due to the width, current speed, and extreme fluctuations of the river (Leopold 1959, p. 381).

I found 35 beaver dens along 26 km of intensively searched riverbank. Thirty-four (97.1%) were on the Park side of the river. Sixteen (45.7%) were active when found. Den entrances were located most often in silty soil at the base of common or giant reeds where the current speed was fast or intermediate (Fig. 11). Common and giant

Table 9. Mean distance (m) traveled by beaver to fell trees in 5 colonies in Big Bend National Park, Texas, November 1980 - May 1981.

	Beaver colony				
Tree species	HSP[1]	PUM[2]	RES[3]	SEC[4]	SER[5]
Acacia			13.12		
Baccharis	25.80	3.99	5.32	20.40	10.72
Desert willow	20.00				
Burrobrush	19.80	12.00		26.69	
Wild tobacco tree					45.00
Willow		6.60		23.49	25.81
Tamarisk	11.76	3.25	7.87	3.83	9.64

[1] Hot Springs colony located in Hot Springs Canyon.

[2] Pumphouse colony located in Rio Grande Village.

[3] Research Station colony located at Boquillas Crossing.

[4] Santa Elena Canyon colony located at the mouth of Santa Elena Canyon.

[5] Santa Elena Roadside colony located 1.6 km downstream from the mouth of Santa Elena Canyon.

Table 10. Prediction equations for dry weight (g) of bark based on diameter (cm), and r^2 values for models for willow, baccharis, and tamarisk trees in Big Bend National Park, Texas.

Species	Prediction equation	r^2 for model
Willow	$WT = 9.60778815 + 2.36188742(DIAM^3)$	0.970937
Baccharis	$WT = 5.11426742 + 3.09084180(DIAM^3)$	0.950982
Tamarisk	$WT = 2.17989200 + 4.55453918(DIAM^3)$	0.969225

Table 11. Percentages of available food (grams of dry bark) from felled baccharis, willow, and tamarisk trees within 5 beaver colonies in Big Bend National Park, Texas, November 1980 - May 1981.

	Beaver colony				
Tree species	HSP[1]	PUM[2]	RES[3]	SEC[4]	SER[5]
Baccharis	7.63	10.16	75.39	3.05	5.92
Willow	0.00	86.64	0.00	95.94	89.77
Tamarisk	92.37	3.20	24.61	1.01	4.30
Total	100.00	100.00	100.00	100.00	99.99

[1] Hot Springs colony located in Hot Springs Canyon.

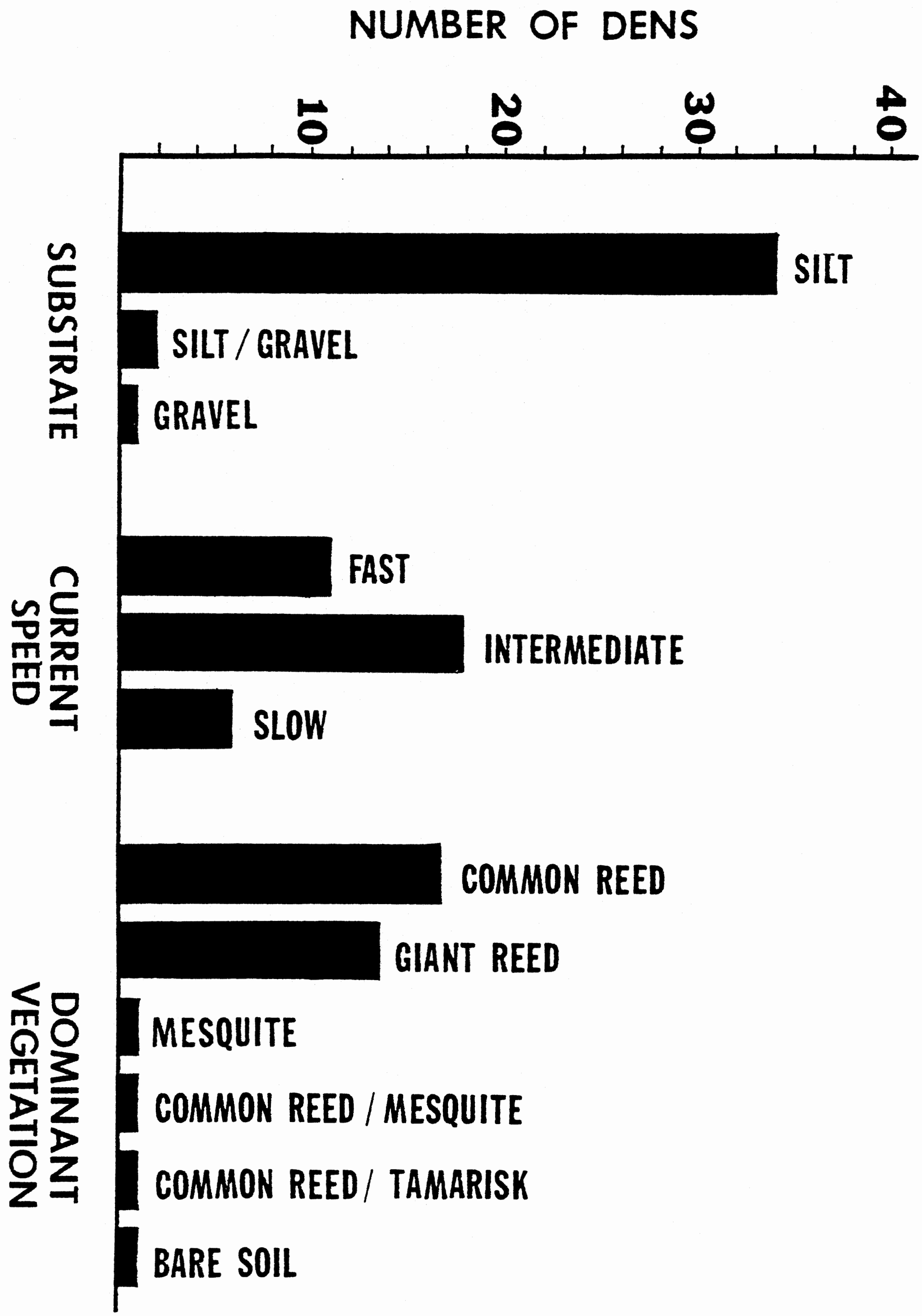
[2] Pumphouse colony located in Rio Grande Village.

[3] Research Station colony located at Boquillas Crossing.

[4] Santa Elena Canyon colony located at the mouth of Santa Elena Canyon.

[5] Santa Elena Roadside colony located 1.6 km downstream from the mouth of Santa Elena Canyon.

Fig. 11. Characteristics of substrate, current speed, and dominant vegetation for 35 beaver dens, Terlingua Creek to Castolon and Old San Vicente to Boquillas Canyon, Big Bend National Park, Texas, 1980–1981.


NUMBER OF DENS
10
20
30
40
SUBSTRATE
SILT
SILT / GRAVEL
GRAVEL
CURRENT SPEED
FAST
INTERMEDIATE
SLOW
DOMINANT VEGETATION
COMMON REED
GIANT REED
MESQUITE
COMMON REED / MESQUITE
COMMON REED / TAMARISK
BARE SOIL

reeds grow in sand and silt up to the river's edge and often overhang the water. Den entrances were usually obscured from view by overhanging reed stalks. The root systems of the reeds are extensive and tough and provide stability to otherwise easily eroded soil. Connor and Feeley (unpubl. rep.) reported 10 of 19 active burrows on the Rio Grande in the Park were located at the base of common reeds. Although seemingly suitable habitat for den sites existed on the Mexican riverbank, I found only 1 den. No dens were found in activity areas in the 3 major river canyons.

The mean diameter of den entrances was 0.43 m. The extremes were 0.22 and 1.00 m. The lengths of the tunnels were 0.3- > 3.0 m. Six (17.1%) dens had tunnels > 3 m long. The mean length for tunnels ≤ 3 m was 1.29 ± 0.60 m. Tunnels commonly opened into larger chambers.

Beaver often used more than 1 den excavated at different levels on the riverbanks. Five dens were used at the HSP colony, 8 at the SER colony, 3 at the RES colony, and 6 at the PUM colony. Active dens were 0.2 m below to 1.5 m above the river level when measured. The mean was 0.30 m above river level, but may not be representative of all active dens because dens with completely submerged entrances were not found.

Beaver were occasionally observed resting on the riverbanks and were flushed several times during daylight hours. Beaver were observed sleeping on the riverbank on 2 occasions. On 30 September 1980 I saw 1 beaver at 1010 sleeping on the riverbank at the HSP colony. The resting site was in the cover of common reeds 2 m above the river and 30 m upstream from the most recently used den site. Another beaver was observed sleeping in a small depression under overhanging reeds 1 m from the river at the Santa Elena Roadside colony. Johnson (1921) described shallow depressions or forms that beaver used as resting and sunning places.

DISCUSSION

Cottonwood Taxonomy

Disagreements regarding the taxonomy of native cottonwoods in Big Bend National Park have occurred. McDougall and Sperry (1951) identified them as Palmer cottonwood (*P. palmeri* Sarg.) as did Schmidly and Ditton (1976). Wauer (1980, p. 24) referred to the cottonwoods at Santa Elena Crossing and Terlingua Abaja as lanceleaf cottonwood (*P. acuminata* Rydb.). Connor and Feeley (unpubl. rep.) reported that only Fremont cottonwood was found in the Park.

Most recently, Eckenwalder (1977) described North American cottonwoods of the sections Abaso and Aigeiros. His treatment lumped all cottonwoods of these sections into 2 species, *P. deltoides* and *P. fremontii*. Native cottonwoods of the American Southwest are currently recognized as subspecies of *P. fremontii*.

Effects of Beaver on Cottonwood Regeneration

Root sprouts and epicormic shoots are regenerative structures frequently observed when the overstory is open and sunlight is able to penetrate to the forest floor (Kozlowski 1971, p. 184). Root sprouts arise from adventitious buds and epicormic shoots from dormant buds. Because these shoots are shade intolerant, the overstory of the parent tree must allow light penetration for growth to take place. Dry soil conditions may have had a detrimental effect on root sprouting and seedling initiation at cottonwood sites with little regeneration.

Cottonwoods at Terlingua Abaja, where the overstory was open, showed the greatest amount of regenerative growth.

Beaver cutting appeared to stimulate epicormic shoot and root sprout growth in cottonwoods. Sprouting after beaver use is well documented (Jackson 1953, Hall 1960, Brenner 1962). Jackson's (1953) data indicated a greater probability of survival of sprouts for trees > 1 in. diameter. Most cottonwoods felled by beaver in the Park were greater than this size class.

Frequency of cutting by beaver influences tree vigor. Hall (1960) emphasized the significance of overbrowsing on the vigor of willow stands. When regenerative shoots were continually cut by beaver on the same stump, the plant eventually died (Jackson 1954). A potential for decreased stand vigor exists at Santa Elena Crossing, Río Vista, and Terlingua Abaja because of heavy beaver use.

Effects of Disturbance Factors

Evidence of visitor use was seen throughout the Park along the floodplain. However, areas along the river were relatively inaccessible and disturbance by Park visitors was generally low. River use by canoeists and rafters has increased in recent years, resulting in heavy use of popular river campsites. Use by Mexican ranchers was negligible, except when associated with trespass livestock activity. Human use did not appear to have negative effects at cottonwood sites. Activity areas of beaver appeared affected by human influence at 5 sites; the 3 border crossings near the Mexican villages of Santa Elena, San Vicente, and Boquillas, and at 2 developed areas with campgrounds adjacent to the river in the Park at Río Grande Village and Castolon. Beaver occupied territories near all these sites, but did not use the food resources. River use by Park visitors may have temporarily disrupted beaver activity patterns when camping occurred near feeding sites. I observed this type of human disturbance during float counts conducted between Santa Elena Canyon and Castolon, in Hot Springs Canyon, and in Rio Grande Village.

Livestock trespassing occurred throughout the floodplain. A network of trails trampled by livestock was evident at several sites Grazing on young shoots of cottonwood and willow was heavy. Glinski (1977) reported that cottonwood reproduction was nearly absent in areas grazed by cattle, and that cattle grazing was the most obvious factor inhibiting cottonwood regeneration in Arizona. Although cottonwood regeneration at Santa Elena Crossing and Rio Vista was higher than at other sites, livestock disturbance had an overall negative effect on cottonwood regeneration.

Tamarisk invasion on the Rio Grande floodplain is extensive and has influenced native flora and fauna. Reduction in the number of native cottonwood and willow stands has been noted. Willow appears to be competing more successfully with tamarisk than cottonwood. However, as tamarisk invades the floodplain and forms dense stands, the number of areas suitable for colonization by willow is reduced. Floodplain fauna may be negatively affected by the spread of tamarisk. Beaver did not fell trees in dense tamarisk stands. Anderson et al. (1977) suggested that saltcedar (tamarisk) communities did not compare favorably with native cottonwood-willow communities in their value to avifauna. Other serious effects of tamarisk invasion are interference with drainage and promotion of flooding, and extensive loss of water through evapotranspiration (Ranwell 1967).

Food Habits

Hall (1960) found that almost every available woody species was cut by beaver in a California colony. Despite their diverse diet, the major foods of beaver over most of their range are aspen (*P. tremuloides* and *P. grandidentata*), cottonwood, and willow (Bradt 1938, Martin et al. 1951, p. 235, Rue 1964, p. 106).

Connor and Feeley (unpubl. rep.) and Swepston (1976) reported major food items of beaver in and near Big Bend National Park. Feeley and Connor (1977, unpubl. rep., Big Bend National Park, Texas) listed foods of beaver in January in order of preference as sedges, willow, cottonwood, tamarisk, acacia, and wild tobacco tree. They reported heavy use of sedges. During this study, beaver grazed on sedges in Hot Springs Canyon in June and July 1980. No other use of sedge was recorded even though it was fairly common throughout the study area. Willow seemed to be the preferred food item of beaver. Willow is recognized as a major food item throughout beaver range in North America (Bradt 1938, Shadle et al. 1943, Hall 1960, Northcott 1971) including Big Bend National Park and similar habitats in other parts of the Southwest (Ffolliot et al. 1976, Swepston 1976, Schmidly 1977, p. 94).

Some mention of other food items eaten by beaver in the Southwest has been made in recent literature. Jackson (1954) noted beaver use of tamarisk in Arizona. Connor and Feeley (unpubl. rep.) recorded Mormon tea as a food item of beaver in the Park. Jackson (1953) documented beaver use of fragrant ash and baccharis in Arizona and added mesquite in later investigations (Jackson 1954). Connor and Feeley (unpubl. rep.) noted beaver use of baccharis in the Park, but lumped it into a group with true willows. No mention of burrobrush or desert willow as beaver foods has been made in recent literature.

The 5 beaver colonies monitored for feeding activity varied greatly in habitat structure, and consequently, use of food resources varied among colonies. The 5 territories were not representative of all beaver habitat in the Park, thus, care must be taken in making inferences regarding food habits of beaver throughout the Park.

Aldous (1938), Hodgdon and Hunt (1953), and Hall (1960) reported that beaver preferred trees approximately 2 in. (5.08 cm) diameter. I examined the results of stand composition and beaver use of 2 willow stands in Rio Grande Village for preference of trees 1.5-2.5 in. diameter. I tested the null hypothesis that beaver felled trees in proportion to their availability by diameter class. The null hypothesis was rejected at the 5 percent level of significance (Chi-square $\underline{P} > 0.005$ at both sites). Beaver felled willow trees 1.5-2.5 in. in much greater proportion than their availability. My results indicated that beaver preferred willow trees approximately 2 in. diameter.

Qualitative observations indicate a similar tendency for baccharis. Conversely, it appeared that beaver preferred smaller diameter tamarisk trees. Trees < 2 cm composed 89.1 percent of all felled tamarisk trees in the 5 colonies. Feeley and Connor (unpubl. rep.) suggested that young tamarisk trees may have lesser salt concentrations than older and larger trees, making them more palatable to beaver.

The proportions of trees felled in various diameter classes were not completely indicative of the importance of the trees in those diameter classes to beaver in terms of food. Small diameter trees probably do not have as much bark as large diameter trees, but the relationship between bark weight and diameter was not known. Aldous

(1938) derived curves for the regression of bark weight on tree diameter for aspen, but there were no reports for willow, baccharis, or tamarisk.

My equations predicted the amount of available food in grams of dry bark for willow, baccharis, and tamarisk for the 5 colonies, but because small trees were generally eaten more completely than large trees (Aldous 1938, Bradt 1938), the actual proportions of food eaten from these species could not be calculated. However, proportions based on number of felled stems (Table 6) and those based on dry weight of bark on felled stems (Table 11) for each species should be limits of intervals that contain the value of the actual proportion eaten by beaver.

Some inferences concerning beaver's diet based on the major food item eaten at each colony in the Park were made in December 1980. It appeared that willow was the major food item for 44 percent of the beaver population, baccharis for 46 percent, and tamarisk for 5 percent. Acacia, cottonwood, and common reed, comprised the remaining 5 percent.

Diet probably affects reproductive potential by its influence on physical condition. Huey (1956) collected reproductive tracts of pregnant female beaver in New Mexico. The average number of embryos per female was 4.2 for aspen habitat types, 2.75 for cottonwood, and 2.06 for willow. Aspen was considered the optimal habitat type. Although productivity was not addressed in this study, productivity of beaver may be low along the Rio Grande where willow, baccharis, and tamarisk are the major food items.

Den Sites

Northern beaver excavate bank dens in addition to building lodges. Southwestern beaver generally do not build lodges on low altitude streams. Little evidence of lodge construction along the Rio Grande was noted. Beaver occupied 3 spring-fed swamps close to the river in Rio Grande Village, but constructed a lodge at only 1. Bank dens were used at other sites.

No dens were found in large river canyons. Beaver in canyon colonies may use resting places on siltbars or among rocks instead of excavating dens because suitable habitat may be limited and predators are noticeably absent. Grater (1936) did not find den sites among rocky riverbanks on the Colorado River in Grand Canyon National Park and hypothesized shelter use among the rocks.

Within colonies, dens were used for different purposes. Use may have been related to tunnel length. Four of 5 frequently observed colonies had 1 active den $>$ 3 m long at some time during the study period. Observations suggested these dens were occupied by adult female beaver during parturition and for a period of time afterward while caring for the kits. In August 1980 an adult female and her kit used a den with a tunnel $>$ 3.0 m long at the Research Station colony site. Two medium-sized beaver believed to be yearlings also used the den. A large adult male used a shallow den 30 m downstream during the same period. Shallow dens may be "bachelor" dens. The adult male is commonly evicted from the main den during parturition (Rue 1964, p. 31).

Effects of River Level Fluctuations

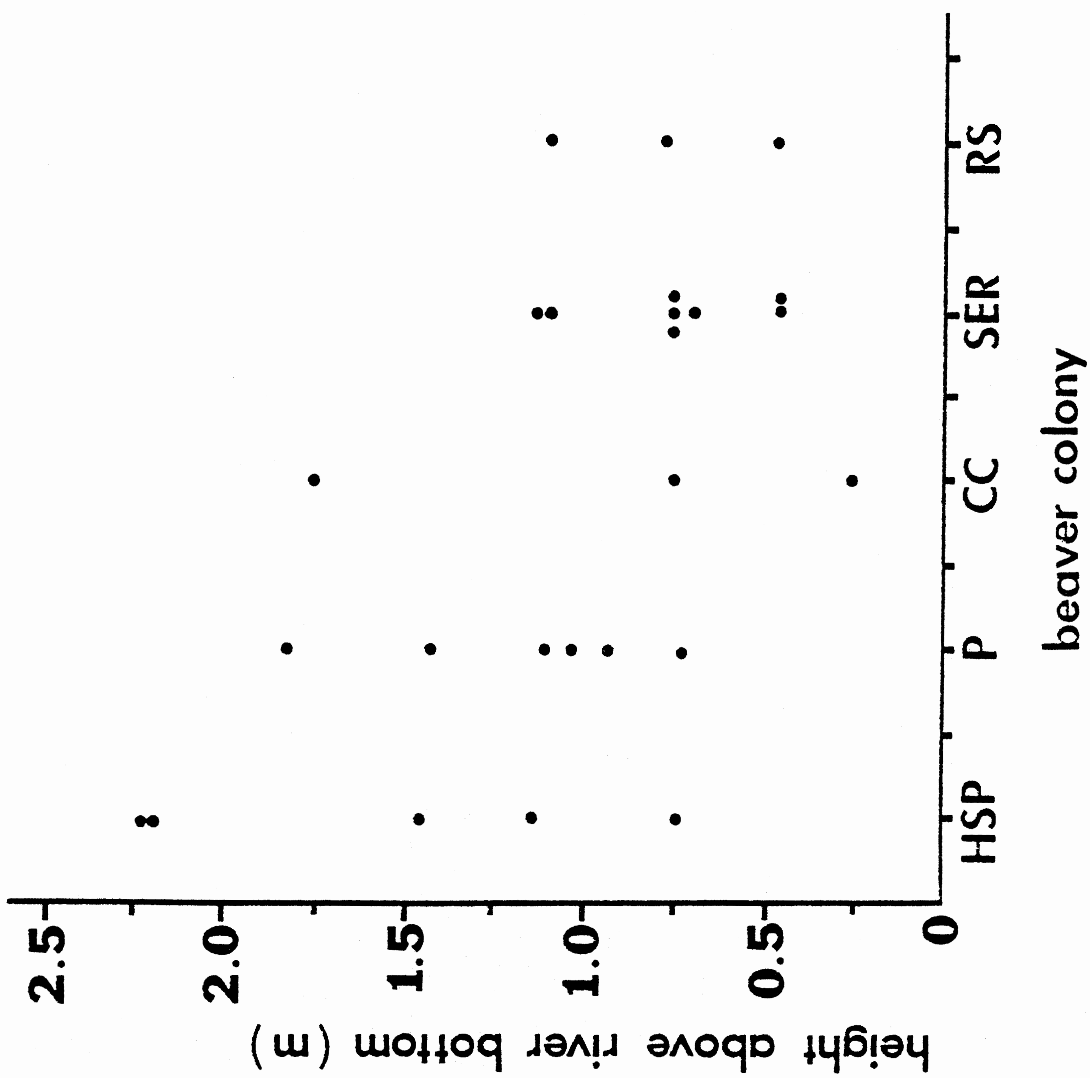
Beaver construct dams to control the water level of an occupied pond. As a result, they are able to build lodges and decrease overland distance to their food sources. Beaver do not build dams on the Rio Grande. The river fluctuates widely due to sporadic heavy rains.

Flooding may have influenced den site locations within colonies because den site locations on the riverbanks varied (Fig. 12) with river level changes. Newly excavated dens were often found high on the riverbank after flooding. Signs of activity indicated use during high water. Beaver abandoned dens after river levels dropped. The riverbank was exposed during periods of low water flow, revealing newly excavated dens and remnants of previously used dens. It appeared that beaver excavated new dens during changes in river levels. No evidence of reoccupation of old den sites was observed.

Beaver also responded to flooding by seeking refuge on the riverbanks. On several occassions beaver were observed resting on the riverbanks after abrupt rises in river level. Beaver also rested in a small cross-canyon that filled with water during flooding.

Flooding appeared to have an effect on beaver use of cottonwoods. As the river level rose and covered the floodplain, beaver were able to reach more of the food resources. Gullies and arroyos running throughout the cottonwood stand at Santa Elena Crossing were filled with water during flooding. Tracks and cut stems confirmed that beaver used these waterways as canals. In late summer and fall flooding covered the floodplain at Rio Vista and decreased distances from the river to the cottonwood trees. Increased beaver activity was noted. Beaver continued to fell cottonwoods at Rio Vista after floodwaters receded, but eventually discontinued activity there.

Fig. 12. Heights (m) of den entrances above the river bottom for 5 beaver colonies on the Rio Grande, Big Bend National Park, Texas, 1980–1981.


height above river bottom (m)
2.5
2.0
1.5
1.0
0.5
0
HSP
P
CC
SER
RS
beaver colony

CONCLUSIONS

The results of this study indicate that beaver-cottonwood interactions on the Rio Grande floodplain in Big Bend National Park are limited by the small number of native cottonwoods and their distance from the river. Although beaver are damaging cottonwoods, I suggest that the current level of use is not harmful to the cottonwood population. The larger number of regenerative structures on trees damaged by beaver vs. undamaged trees supports this hypothesis. Beaver are not felling enough cottonwoods to threaten the existence of the native cottonwood population.

Although beaver densities along the Rio Grande are low, the population in Big Bend National Park is well established. Beaver have adapted to this ecosystem by heavily exploiting the willow resource and by occasionally eating large proportions of less desirable food items. Structurally sound dens at various levels on the riverbank represent successful adaptation to widely fluctuating river levels.

The floodplain community along the Rio Grande in the Park has been negatively influenced by several disturbance factors. Native flora and fauna, including cottonwood, willow, and beaver, are receiving increased pressure from human and livestock disturbances. In the last 30 years tamarisk has spread throughout the floodplain and displaced much of the native vegetation. The spread of tamarisk can be expected to increase in the future unless an intensive eradication program is implemented by the Park. Complete eradication may be economically impossible, but the role of tamarisk in eliminating standing water in xeric habitats should not be ignored. Additional attention to these problems are needed if negative impacts influencing this system are to be minimized.

SUMMARY

Beaver-cottonwood interactions and beaver ecology were investigated in Big Bend National Park, Texas, June 1980 through May 1981. Major findings were:

1. Approximately 232 native cottonwoods grew at 8 sites on the United States floodplain adjacent to the Rio Grande in the Park. At least 29 (12.5%) cottonwoods were damaged by beaver. Beaver appeared to prefer small diameter cottonwood trees close to the river. Tree felling by beaver increased the number of regenerative shoots.

2. Willows grew at 32 distinct sites on the U.S. floodplain. Stands were made up mostly of small diameter trees. Beaver use of willow was extensive.

3. Forty-three distinct areas of beaver activity comprising 54 colonies were located along 131 km of river. The areas of activity made up 45.8 percent of the study area. Most activity occurred on the U.S. floodplain. Most activity areas were adjacent to dense vegetation on broad, flat sections of the floodplain. Six (14.3%) were in river canyons. No dams or lodges were constructed along the river.

4. I estimated 134 beaver inhabited the study area, an average of 1.02 beaver/km of river, 2.23 beaver/km of occupied habitat, and 2.48 beaver/colony. The greatest density of beaver for a stretch of river $>$ 2 km long was 3.25 beaver/km.

5. Beaver ate a variety of woody and herbaceous plants, some unique to southwestern riparian ecosystems. The most common food items were willow, baccharis, and tamarisk. Beaver traveled up to 120 m from the river to fell trees. The mean distance traveled to obtain food in 5 colonies was 15 m. Large variability in distances traveled within and

among colonies resulted from heterogeneity in habitat structure. The mean diameter of woody species cut by beaver in 5 colonies was 1.63 cm. Mean diameters of felled trees varied among species, colonies, and distances from the river. Of the 3 most commonly felled tree species, willow and baccharis were cut more often in large diameter classes. Beaver appeared to prefer small diameter tamarisk trees and rarely cut trees > 2.0 cm dbh.

6. Prediction equations for dry weight of bark based on tree diameter were derived for willow, baccharis, and tamarisk trees. An estimate of the amount of food obtained from each species in 5 colonies was made. Willow made up the bulk of the diet for approximately 44 percent of the beaver in the Park in December 1980, baccharis for 46 percent, and tamarisk for 5 percent. Cottonwood was not a major food for beaver in the Park.

7. Beaver excavated bank burrows most commonly in silty soil at the base of common and giant reeds on the U.S. floodplain. Constantly fluctuating river levels influenced the excavation of more than 1 den at various levels on the riverbank in most colonies.

8. Beaver have adapted to southwestern riparian ecosystems despite less than optimal habitat, the presence of disturbance factors, and extreme environmental conditions.

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