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Causes and Consequences of Mammal Species Richness

SIX

Overview

The San Pedro watershed is an internationally recognized "hotspot" for mammals, hosting one of the richest assemblages of mammal species in the United States (Simpson 1964, Hall 1981, Duncan 1988). Estimates of species richness range from 61 to 87 mammals, about half of the highest estimate in the world (139 mammals in Cocha Cashu/Pakitza, a Neotropical lowland rainforest site; Voss and Emmons 1996). These estimates are particularly high for a semi-arid habitat at this latitude (Boeer and Schmidly 1977). In this chapter, we consider the importance of geography, environmental gradients, and non-equilibrium processes in explaining the extensive mammalian diversity of the San Pedro watershed.

In the sections that follow, we review definitions of richness and diversity, provide some background on the mammal fauna of the San Pedro, describe broad ecological theories relating abiotic and biotic factors to species richness, and apply these to the San Pedro watershed with mammals as a case study. We close with a discussion of how mammals may (in turn) affect the habitats in which they live and a brief section on the impacts of human activity on the mammals of the San Pedro watershed.

Definitions of Species Richness and Diversity

According to Krebs (1999), species diversity is the total number of species weighted by their relative abundance. It includes two components: species richness, which refers to the total number of species in a community, and species evenness, which refers to the relative number of individuals of each species in a community. Thus, a community with 100 species is more species rich than one with 50 species. Likewise, a community in which the species are equally abundant is more even than one dominated by one or a few species. Although other definitions exist, in this chapter we adhere to Krebs's definitions of diversity, richness, and evenness.

Whittaker (1972) partitioned total species richness in a region, called gamma richness, into two components: local (alpha) richness and turnover of species between localities (beta richness), where Gamma Richness = Alpha Richness × Beta Richness. How one defines a locality depends on the question being asked and the taxon under consideration. Since localities can vary in size, scale plays an important role in any discussion of species richness (Sarr et al. 2005). In this chapter we treat each habitat type as a locality and use beta richness to refer to differences in species composition among habitats. Scale also affects calculations of species evenness. Clumped and/or random distributions of organisms provide different estimates of species evenness depending on the scale of measurement and the index being used (Wilson et al. 1999). For example, if a few sample quadrats happened to fall on clumps of a patchily distributed species, one would overestimate its abundance in the community.

Researchers have developed different diversity metrics to suit their needs. Commonly used metrics include the Simpson's Diversity Index and the Shannon-Wiener Diversity Function (Krebs 1999). Similarly, many different measures of evenness have been proposed, with no single index standing out as the best one. For simplicity, we will focus our discussion on species richness.

Mammals of the San Pedro

The number of mammal species that occur in the San Pedro watershed—estimated using indirect observations (e.g., sign and scat), captures, or field observations (Woolsey 1987, Duncan 1988, Hass 2001), as well as overlapping range maps (Cockrum 1960, Hall 1981, Davis 1982, Hoffmeister 1986)—may be as high as 87 species (see tables 6.1 and 6.2). Excluding extirpated species, and using only observations and occurrence records but not range maps, a more conservative estimate is 61 species (Woolsey 1987, Duncan 1988, Hass 2001) (table 6.1). By way of comparison, Boeer and Schmidly (1977) listed only 30 mammal species on the lower Rio Grande at Big Bend National Park, while 55 species are confirmed in the Bill Williams River National Wildlife

Refuge (K. Blair, personal communication). Estimates for mammal species richness in the nearby Verde River watershed range as high as 92 (but this includes humans, extirpated species, and subspecies; L. Stevens, personal communication). The 61 mammal species observed in the San Pedro watershed include 1 didelphid marsupial (order Didelphimorphia), 1 insectivore (order Insectivora), 29 rodents (order Rodentia), 3 lagomorphs (rabbits and hares, order Lagomorpha), 8 bats (order Chiroptera), 3 artiodactyls (even-toed ungulates, order Artiodactyla), and 16 carnivores (order Carnivora) (Woolsey 1987, Duncan 1988, Hass 2001) (table 6.1).

Among the species that have been regionally or locally extirpated are three top predators—the grizzly bear, jaguar, and gray wolf (Ceballos 1985, Duncan 1988, Hass 2001). However, recent jaguar sightings in southern and southeastern Arizona suggest that source populations are nearby and could potentially recolonize the San Pedro watershed. Likewise, gray wolves have been reintroduced in eastern Arizona, not too far from the San Pedro watershed. The long-tailed weasel has not been detected in the area since the 1950s (Hoffmeister and Goodpastor 1954, Woolsey 1987), and black-tailed prairie dogs were last sighted on the U.S. side of the border in 1938 (Hoffmeister 1986), though they still occupy the San Pedro watershed south of the Mexican border (Castillo-Gamez et al. 2005). Beavers were extirpated from the upper San Pedro River by the mid-1980s (Ceballos 1985, Duncan 1988). A small beaver population has recolonized reaches near the San Pedro's confluence with the Gila River, and several beaver were recently reintroduced to suitable habitats along the upper parts of the river. Muskrats have not been recorded along the San Pedro River since the 1890s (Allen 1895), but could possibly survive if reintroduced (Duncan 1988). River otters have not been detected for a long time, but were once widely distributed across the Southwest and likely occupied parts of the San Pedro watershed (Woolsey 1987).

Theory of Species Richness

Although no single explanation suffices, ecologists have found relationships between species richness and a host of environmental variables including latitude, climate, biological productivity, stress, disturbance, habitat heterogeneity, habitat complexity, and ecosystem size and isolation (MacArthur 1972, Whittaker 1975, Schluter and Ricklefs 1993, Brown 1995, Rosenzweig 1995). More specifically, species richness tends to increase with decreasing latitude (Latham and Ricklefs 1993), increasing area (Hamilton et al. 1963), decreasing isolation (Simberloff and Wilson 1969), increasing temperature and precipitation (Richerson and Lum 1980), increasing habitat heterogeneity (Simpson 1964) and habitat complexity (MacArthur and MacArthur 1961), and intermediate levels of disturbance and environmental stress (Connell 1978, Menge and Sutherland 1987). Thus, both geographic position and

TABLE 6.1. Mammal species of the San Pedro River.

Introduced species names are marked with an asterisk (*); extirpated species names are shaded gray.

Family	Common name	Scientific name
Didelphidae	Virginia opossum	*Didelphis virginiana*
Soricidae	Desert shrew	*Notiosorex crawfordi*
Phyllostomatidae	California leaf-nosed bat	*Macrotus californicus*
Vespertilionidae	Pallid bat	*Antrozous pallidus*
	Big brown bat	*Eptesicus fuscus*
	Red bat	*Lasiurus borealis*
	Cave myotis	*Myotis velifer*
	Townsend's big-eared bat	*Plecotus townsendi*
Molossidae	Western bonneted bat	*Eumops perotis*
	Mexican free-tailed bat	*Tadarida brasiliensis*
Leporidae	Antelope jack rabbit	*Lepus alleni*
	Black-tailed jack rabbit	*Lepus californicus*
	Desert cottontail	*Sylvilagus audubonii*
Sciuridae	Harris's antelope squirrel	*Ammospermophilus harrisii*
	Black-tailed prairie dog	*Cynomys ludovicianus*
	Spotted ground squirrel	*Spermophilus spilosoma*
	Round-tailed ground squirrel	*Spermophilus tereticaudus*
	Rock squirrel	*Spermophilus variegatus*
Geomyidae	Botta's pocket gopher	*Thomomys bottae*
Heteromyidae	Bailey's pocket mouse	*Chaetodipus baileyi*
	Hispid pocket mouse	*Chaetodipus hispidus*
	Rock pocket mouse	*Chaetodipus intermedius*
	Desert pocket mouse	*Chaetodipus penicillatus*
	Merriam's kangaroo rat	*Dipodomys merriami*
	Ord's kangaroo rat	*Dipodomys ordii*
	Banner-tailed kangaroo rat	*Dipodomys spectabilis*
Cricetidae	White-throated wood rat	*Neotoma albigula*
	Muskrat	*Ondatra zibethicus*
	Northern grasshopper mouse	*Onychomys leucogaster*
	Southern grasshopper mouse	*Onychomys torridus*
	Brush mouse	*Peromyscus boylii*
	Cactus mouse	*Peromyscus eremicus*
	White-footed mouse	*Peromyscus leucopus*

TABLE 6.1. *(continued)*

Family	Common name	Scientific name
Cricetidae *(cont.)*	Deer mouse	*Peromyscus maniculatus*
	Fulvous harvest mouse	*Reithrodontomys fulvescens*
	Western harvest mouse	*Reithrodontomys megalotis*
	Plains harvest mouse	*Reithrodontomys montanus*
	Arizona cotton rat	*Sigmodon arizonae*
	Fulvous cotton rat	*Sigmodon fulviventer*
	Yellow-nosed cotton rat	*Sigmodon ochrognathus*
Muridae	House mouse*	*Mus musculus**
Erithizontidae	Porcupine	*Erithizon dorsatum*
Castoridae	Beaver	*Castor canadensis*
Cervidae	Mule deer	*Odocoileus hemionus*
	White-tailed deer	*Odocoileus virginianus*
Tayassuidae	Collared peccary	*Pecari tajacu*
Procyonidae	Ringtail	*Bassariscus astutus*
	White-nosed coati	*Nasua narica*
	Northern raccoon	*Procyon lotor*
Mephitidae	Common hog-nosed skunk	*Conepatus mesoleucus*
	Hooded skunk	*Mephitis macroura*
	Striped skunk	*Mephitis mephitis*
	Western spotted skunk	*Spilogale gracilis*
Mustelidae	Northern river otter	*Lontra canadensis*
	Long-tailed weasel	*Mustela frenata*
	American badger	*Taxidea taxus*
Canidae	Domesticated dog*	*Canis familiaris**
	Coyote	*Canis latrans*
	Gray wolf	*Canis lupus*
	Gray fox	*Urocyon cinereoargenteus*
	Kit fox	*Vulpes macrotis*
Felidae	Domesticated cat*	*Felis silvestris**
	Bobcat	*Lynx rufus*
	Jaguar	*Panthera onca*
	Puma	*Puma concolor*
Ursidae	Black bear	*Ursus americanus*
	Grizzly bear	*Ursus arctos*

Note: Documented by captures, observations, and occurrence records (64 native species [6 extirpated] and 3 non-native species) based on Woolsey (1987), Duncan (1988), and Hass (2001).

TABLE 6.2. Mammal species with range maps that overlap the San Pedro riparian corridor.

Not documented by captures, observations, or occurrence records (20 species).

Family	Common name	Scientific name
Phyllostomatidae	Mexican long-tongued bat	*Choeronycteris mexicana*
	Southern long-nosed bat	*Leptonycteris curasoae*
Vespertilionidae	Spotted bat	*Euderma maculatum*
	Allen's big-eared bat	*Idionycteris phyllotis*
	Silver-haired bat	*Lasionycteris noctivagans*
	Hoary bat	*Lasiurus cinereus*
	Southern yellow bat	*Lasiurus ega*
	Southwestern myotis	*Myotis auriculus*
	California myotis	*Myotis californicus*
	Small-footed myotis	*Myotis ciliolabrum*
	Fringed myotis	*Myotis thysanodes*
	Long-legged myotis	*Myotis volans*
	Yuma myotis	*Myotis yumanensis*
	Western pipistrelle	*Pipistrellus hesperus*
Molossidae	Pocketed free-tailed bat	*Nyctinomops femorosaccus*
	Big free-tailed bat	*Nyctinomops macrotis*
Heteromyidae	Silky pocket mouse	*Perognathus flavus*
Muridae	Northern pigmy mouse	*Baiomys taylori*
Antilocapridae	Pronghorn	*Antilocapra americana*
Felidae	Ocelot	*Leopardus pardalis*

Source: Based on Duncan (1988).

local environmental conditions likely influence species richness. Historical factors (both natural and anthropogenic) have profound effects as well.

The tendency towards higher species richness at lower latitudes has received considerable attention but cannot be easily explained, in large part due to the host of factors (climate, geography, etc.) that vary in parallel with latitude (Schluter and Ricklefs 1993). The relationship between species richness and climate appears much clearer—conditions that favor biological production in terrestrial ecosystems (warm temperatures and abundant precipitation) often correlate with high species richness (Richerson and Lum 1980). High levels of productivity may not always maximize species richness, however; the relationship appears to be far more complex than a simple linear association. Other factors such as landscape position, seasonality, and species interactions affect both primary production and species richness (Whittaker 1975, Huston 1994, Brown 1995, Schade et al. 2003), leading to neutral or even inverse relationships between productivity and species rich-

ness, depending on the scale of observation. Thus, many studies have found that species richness increases with increasing production when species are sampled at large spatial scales. However, when sampled at smaller scales, species richness often peaks at intermediate levels of productivity.

Habitat heterogeneity refers to the number of different habitat types within a given area. Topographic and geomorphic variation combine with variation in temperature and water availability to provide diverse abiotic conditions, which, in turn, result in different habitat types. Because different species often favor particular habitats, a diversity of habitats results in high beta richness and has been cited as one of the reasons for the high levels of species richness in mountainous regions and riparian habitats (Simpson 1964, Sabo et al. 2005). Habitat complexity refers to vegetation structure within a given habitat, for example, the canopy, understory, and shrub- and ground-level vegetation in a forest make it a complex habitat. This complexity increases alpha richness, the number of species in a given habitat, by providing more niches for species to occupy (MacArthur and MacArthur 1961, Pianka 1967).

Disturbance and environmental stress (sensu Menge and Sutherland 1987) can increase both local and regional species richness (Connell 1978, Huston 1994). Increases in alpha richness at intermediate disturbance levels are thought to represent a trade-off between harsh abiotic conditions eliminating all or most species in a given area when disturbance is frequent (or stress levels are high) and competitive pressure from superior competitors crowding out other species in an area when disturbance is infrequent (or stress levels are low). Beta richness also increases as a result of disturbance, due to the creation of spatial heterogeneity across a landscape (Pollock et al. 1998) and through time. Disturbance resets the successional trajectory of a patch; spatially and temporally variable disturbance (as is characteristic of riparian habitats) results in patches of different seral stages, each containing a different suite of species. For example, riparian areas along the San Pedro River contain habitats ranging from mature cottonwood/willow forests to sparsely vegetated ground; different plant and animal species utilize the different seral stages, increasing the overall richness of the riparian zone.

As described by MacArthur and Wilson (1967), species richness on islands depends on a balance between colonization and extinction, both of which relate to island size and distance to the mainland. Small, isolated islands such as Hawaii are expected to have lower species richness, whereas large islands close to a continent, such as Cuba, are expected to have higher species richness. The theory of metapopulation dynamics extends this thinking to different habitat types in a terrestrial landscape (Hanski 1999). According to the theory, the size and location of habitat patches within

a landscape influence the alpha, beta, and gamma richness of a region. Increasing patch size results in larger populations that are more resistant to extinction. Patch location relative to other patches influences dispersal and the probability of recolonization following extinction events. Together, these two geographic factors play an important role in determining species richness patterns for a given region (Brown 1971, Tonn and Magnuson 1982, Rosenzweig 1995).

Influences on Mammal Species Richness in the San Pedro Watershed

Several of the factors described above combine to produce the high mammal species richness of the San Pedro watershed. These factors include region size, biogeographic location, climate, water availability, primary productivity, habitat heterogeneity, disturbance, and edge habitat use. The factors can be summarized into three broad categories: geography, environmental gradients, and non-equilibrium processes. Any given factor may fall under more than one of these headings; we therefore use them more for heuristic than for classification purposes.

GEOGRAPHY

This category includes factors such as region size, biogeographic setting, and climate. The San Pedro watershed is large (ca. 12,000 km^2), well connected to other species-rich regions, and has a warm temperate climate (see chap. 11). The watershed lies at the intersection of four biogeographic zones (the Sonoran Desert to the west, the Chihuahuan Desert to the east, the Rocky Mountains to the north, and the Sierra Madres to the south) and includes species from each zone. Long summers and relatively mild winters allow mammals with tropical affinities, such as peccaries, coatis, opossums, and various bats, to extend their range northward into the San Pedro watershed (Hoffmeister 1986). Although precipitation is modest, rainfall peaks during late summer, maximizing biological production. Thus, regional conditions resemble those that correlate with high species richness. In sum, the San Pedro watershed is a large, well-connected region with a favorable climate.

ENVIRONMENTAL GRADIENTS

This category includes primary productivity and habitat heterogeneity, both of which are driven, in large part, by streamflow regime and gradients in water availability. In the San Pedro watershed, spatio-temporal variation in water availability is the principal factor constraining primary and secondary productivity (Huxman et al. 2004). Inflowing groundwater sustains permanent stream water and high productivity in some reaches, while in other reaches the stream flows only seasonally. In all reaches, high seasonal and annual

variation in precipitation, flood magnitude, and aquifer recharge (typical of dry regions) creates sharp temporal fluctuations in water availability on the river floodplains and terraces.

Mammal species have evolved physiological and behavioral mechanisms for dealing with variation in resource availability. Heteromyids (e.g., kangaroo rats, pocket mice) have physiological adaptations that allow them to cope with little or no drinking water in their diets (Schmidt-Nielsen 1964, Tracy and Walsberg 2002); moreover, many desert mammals (e.g., ground squirrels, pocket gophers, kangaroo rats, pocket mice, woodrats, etc.) have evolved food-caching behaviors that allow them to endure periods of low resource levels (Vander Wall 1990). Some mammals, such as bats, ground squirrels, deer mice, kangaroo rats, and pocket mice, hibernate, aestivate, or undergo periods of inactivity, often associated with seasonal accumulation of fat (Hudson 1967). Finally, larger, more mobile mammals shift their movement and foraging patterns to areas of relatively higher resource abundance (Valenzuela and Ceballos 2000). For example, coatis in tropical dry forests shift their activity to arroyo forest during dry periods, where arthropods and water are more readily available, and may do the same along the San Pedro. Skunks, foxes, and other carnivores along the San Pedro also shift their diet and movement patterns, tracking the availability of seasonally or spatially abundant foods (Soykan and Sabo, forthcoming).

The vegetation types within the San Pedro watershed vary in plant species composition as well as in amount of cover in different height strata (see chap. 1). Vegetation influences mammal populations by providing food, affecting movement patterns, and providing protection from predators. Since each species has different environmental requirements, many mammals show affinities for particular vegetation types (tables 6.3, 6.4). Along the San Pedro River, five carnivores (bobcat, kit fox, puma, and two species of *Mephitis* skunks) used vegetation types in proportion to their availability, while six others (badger, coyote, gray fox, hog-nosed skunk, coati, and raccoon) showed some habitat affinity, with their sign being found more often than expected in certain habitats (Hass 2001). Some rodents also show habitat affinities. For example, cricetids (e.g., deer mice, wood rats) tend to utilize habitats with dense ground cover characteristic of sacaton grassland, saltcedar, or marsh habitats (Stamp and Ohmart 1979, Duncan 1988, Ellison and Van Riper 1998), while heteromyids (e.g., kangaroo rats, pocket mice) generally prefer more open vegetation cover characteristic of upland environments (Stamp and Ohmart 1979, Duncan 1988).

Water availability, in particular distance to groundwater, is a principal factor that determines vegetation types along the San Pedro River (see chap. 1). Mammal species vary in their habitat affinities; because of this, spatial variation in water table depth, and the resulting habitat heterogeneity, increases

TABLE 6.3. Common small mammal habitat associations along the San Pedro River.

Values represent the relative density of small mammals for each habitat type (number per 300 trap nights for rodents; number per 100 trap nights for shrews). Shaded cells indicate densities greater than expected based on a uniform distribution among habitats.

	Vegetation association							
Common name	243.30 MSH	223.21 CW	233.221 TAM	223.231 MQ	143.142 SAC/MQ	143.141 SAC	153.20 DS	300.00 AG
Desert pocket mouse	0.0	0.3	7.0	2.8	1.0	0.0	0.9	0.0
Bailey's pocket mouse	0.0	0.0	0.0	2.0	0.0	0.0	0.1	0.0
Merriam's kangaroo rat	0.0	0.0	5.0	1.8	2.0	0.0	8.5	0.0
Plains harvest mouse	1.5	0.0	0.0	0.0	1.6	0.0	0.0	0.0
Western harvest mouse	3.5	0.7	1.0	1.6	4.8	8.5	0.3	0.0
Fulvous harvest mouse	0.5	0.0	1.0	0.0	0.0	0.0	0.1	1.2
Cactus mouse	1.5	2.2	6.0	4.0	0.0	0.0	2.4	0.0
Deer mouse	6.5	6.2	11.0	0.6	8.6	1.0	2.8	5.4
White-footed mouse	28.0	3.7	18.0	0.2	0.0	8.5	0.2	0.0
Northern grasshopper mouse	0.0	0.0	3.0	1.6	0.2	0.0	0.5	0.0
Southern grasshopper mouse	0.0	0.0	0.0	0.0	0.2	0.0	0.9	0.0
Arizona cotton rat	6.0	0.0	0.0	1.2	10.6	6.0	0.0	14.4
White-throated wood rat	1.0	1.8	4.0	3.2	1.2	0.0	3.1	0.0
Desert shrew	NA	24.6	11.8	8.0	11.4	5.9	1.0	NA
Number of Species Captured*	9	9	10	11	10	5	14	4
Number of Plots Sampled	2	6	1	5	5	2	12	5

Source: Based on Duncan 1988 and Duncan and Corman 1991.

Notes: Sampling did not incorporate detection probabilities and was not uniform among habitats—thus, these data must be interpreted with caution. MSH = Chihuahuan Interior Marshland Biome, CW = Cottonwood-Willow Series, TAM = Tamarix-Mixed Deciduous Association, MQ = Mesquite Association, SAC/MQ = Sacaton-Mesquite Association, SAC = Sacaton Association, DS = Chihuahuan Desertscrub Biome, AG = Agricultural Land.

*Total number of small mammal species for each habitat type, including several uncommon species not included in this table.

beta richness in the San Pedro watershed. The wettest habitats along the San Pedro River are marshlands adjacent to perennial water. Five small mammal species (deer mouse, western harvest mouse, plains harvest mouse, Arizona cotton rat, and white-footed mouse) had high abundance in San Pedro marsh habitat, with one (white-footed mouse) being substantially more abundant in marsh than in other habitats (Duncan 1988). Raccoon sign was detected more often than expected in cottonwood/willow forest (Hass 2001), a mesic, floodplain habitat, and desert shrews were two to three times more abundant in cottonwood/willow forests than in tamarisk (saltcedar), sacaton, or mesquite habitats (Duncan and Corman 1991). Several other small mammals (white-footed mouse, cactus mouse, deer mouse, white-throated wood rat) were abundant in cottonwood/willow habitats, but were not considered to be habitat specialists (Duncan 1988). Two small mammal species, desert pocket

TABLE 6.4. Mammalian carnivore habitat preferences along the San Pedro River

Values represent the proportion of total signs for that species encountered in each vegetation type. Shaded cells indicate values greater than expected based on availability.

	Riparian forest	Grassland	Desert scrub	Mountain woodland
Mephitis skunks	0.27	0.17	0.39	0.17
Hog-nosed skunk	0.12	0.19	0.47	0.23
Badger	0.07	0.40	0.40	0.13
Coati	0.11	0.00	0.11	0.78
Northern raccoon	0.47	0.20	0.29	0.04
Kit fox	0.21	0.21	0.50	0.07
Gray fox	0.14	0.15	0.39	0.32
Coyote	0.09	0.30	0.51	0.11
Bobcat	0.31	0.17	0.38	0.14
Puma	0.34	0.16	0.29	0.21

Source: Hass 2001.

Note: Vegetation type was classified according to the predominant vegetation within a 10 m circle surrounding the carnivore sign. Riparian forest included cottonwood/willow/ash gallery forest >5 m high. Mesquite bosques were categorized as desert scrub. Grassland refers to non-riparian grassland habitats found above the river terrace or in the foothills of the Huachuca Mountains.

mouse and southern grasshopper mouse, had substantially higher abundance along the San Pedro in patches of saltcedar/mixed deciduous trees than in other habitat types (Duncan 1988). Along the Rio Grande, both of these rodents have an affinity for saltcedar patches (Stamp and Ohmart 1979).

River terraces of the San Pedro are vegetated by sacaton grassland, mesquite woodland, mesquite savanna, or mixed herbaceous assemblages on abandoned farm fields and are commonly several meters above and 100 to 200 m from the low-flow channel. Several rodents (Bailey's pocket mouse, plains and western harvest mouse, and Arizona cotton rat) and carnivores (coyote, hog-nosed skunk, gray fox, coati, and badger) (fig. 6.1a) were detected more often on terraces than in floodplain habitats (Duncan 1988, Hass 2001). Within the terraces, Bailey's pocket mouse was most common in mesquite habitats (Duncan 1988), though this species was trapped in a variety of habitat types on the Verde River (Stamp and Ohmart 1979), suggesting that habitat affinities can be context dependent. The western harvest mouse was almost twice as abundant in sacaton grasslands as in any other habitat on the San Pedro, consistent with its affinity for dense grassland habitats along other rivers (Falck et al. 2003).

Upland habitats, characterized by Chihuahuan desert scrub (upper basin) or Sonoran desert scrub (lower basin), are located tens to hundreds of meters from the active channel. Due to their unique vegetation and climate,

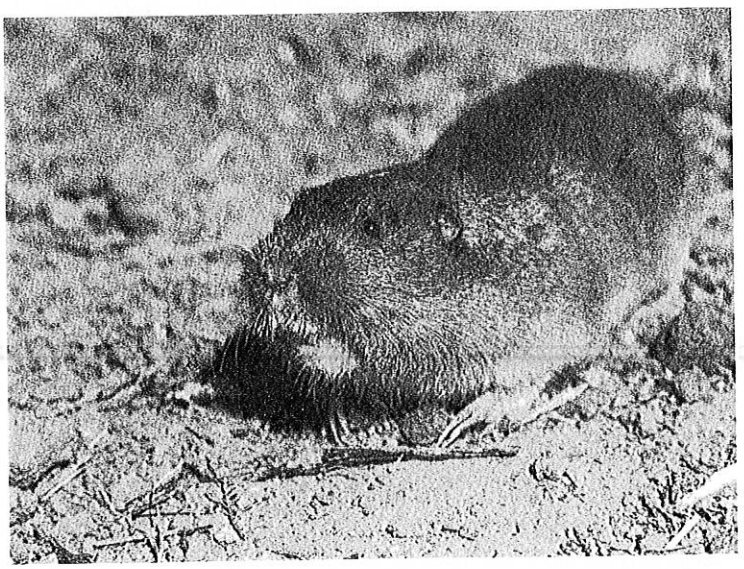


Fig. 6.1. Two earth-dwelling mammals of the San Pedtro riparian corridor: American badger (top; 6.1a) and Botta's pocket gopher (bottom; 6.4b). Photo credits: Robert J. Luce.

they support a different suite of organisms. Two mammal species, Merriam's kangaroo rat and the northern grasshopper mouse, were most common in the Chihuahuan desert scrub habitats studied by Duncan (1988).

Mammal species of desert riparian corridors vary in their reliance on surface water. Wide-ranging carnivores such as puma and black bear probably depend on the river to rehydrate while moving between mountain areas (Hass 2001). Moreover, they utilize washes as movement corridors through inhospitable desert habitats. A number of bat species forage regularly over water (Hinman and Snow 2003). Peccary, raccoon, gray fox, bobcat, and puma and other large mammals breed along the river (Hoffmeister 1986, Duncan 1988, Hass 2001), but it is not known to what extent this is due to the surface water

directly, the effects of water on riparian vegetation type and productivity, or both. Additionally, perennial water sources are important for a number of small mammals such as deer mice and desert shrews (Duncan 1988, Duncan and Corman 1991).

Due to its high habitat heterogeneity, the San Pedro watershed contains a great deal of edge habitat; that is, habitat boundaries separating two distinct vegetation types (e.g., the boundary between mesquite bosques and desert scrub). Ecological boundaries have long been known to affect the distribution and abundance of organisms, and different species can increase or decrease near edges (Ries et al. 2004).

Numerous studies have demonstrated that resource subsidies across ecological edges can affect population and community structure in both habitats (Rose and Polis 1998, Polis et al. 2004). Sabo and Power (2002) found that aquatic insects increased lizard abundance on riparian cobble bars. In turn, by increasing the abundance of predators, a resource subsidy may depress local prey populations that live in the subsidized habitat. For example, Murakami and Nakano (2002) found that aquatic insects increased near-river bird abundance; the birds also foraged on terrestrial insects, decreasing their abundance in near-river habitats.

Although few empirical examples exist, predator movement between habitats has the potential to reduce prey populations, perhaps even leading to prey exclusion from small habitat patches (Oksanen 1990, Cantrell et al. 2001). The abundance of carnivores along the San Pedro River makes it a likely location for this phenomenon, termed spillover predation. Species such as gray fox and striped skunk often live near the river but forage widely across the landscape, potentially reducing prey populations in desert scrub habitats located adjacent to the riparian corridor (Soykan and Sabo, forthcoming).

NON-EQUILIBRIUM PROCESSES

This category, which includes disturbance and subsequent increases in habitat heterogeneity, deals with spatio-temporal variation in the environment and its effects on species richness. Floods cause large changes in surface water depth and distribution and scour vegetation, seeds, and litter from the floodplain. In so doing, floods exert a strong influence on mammal community structure along the San Pedro and other free-flowing desert rivers (Andersen and Nelson 1999). Obligate riparian mammals such as beaver have behavioral and morphological adaptations to the flood regime (Andersen et al. 2000). Large or volant mammals generally have large home ranges and can escape flooded areas. In contrast, small mammal species that facultatively use riparian environments and that have small home ranges may be less tolerant of flooding and thus less able to exploit riparian environments (Andersen et al. 2000). In response to flood events, certain species, such as cactus and

white-footed mice, utilized the canopy as a temporary refuge, though non-arboreal small mammals such as Ord's kangaroo rat experienced high mortality during flood events (Andersen and Nelson 1999, Andersen et al. 2000). Andersen and Nelson (1999) attributed the absence of certain species from cottonwood/willow forests on the lower Colorado and Bill Williams Rivers to an inability to move sufficiently far during periods of flooding.

On rivers such as the lower San Pedro, where flood regimes are characterized by high intensities and frequencies, open areas can cover large portions of the floodplain. This can decrease the available habitat for small mammal species that require dense vegetation cover as protection from predators (Andersen et al. 2000). However, this resetting of the successional process increases habitat heterogeneity in the riparian zone, creating a patchwork of seral stages (Pollock et al. 1998). If species are differentially adapted to exploit the various patches of riparian vegetation, then flooding can lead to high beta richness in the riparian zone. Additionally, woody debris resulting from flood events has been found to increase small mammal species richness, due to lower temperatures within the debris piles and/or protection from predators (Steel et al. 1999). Flood debris also provides materials needed for wood rat midden construction (Ellis et al. 1997, Ellison and Van Riper 1998). Thus, through its indirect effects on vegetation structure (patch dynamics, large woody debris accumulation), flooding profoundly influences mammal species richness and abundance along the San Pedro River.

Fire is another disturbance factor in riparian zones such as the San Pedro that develops seasonally dry understory vegetation. Some small mammals avoid direct heat by burrowing into the soil, while larger and more mobile animals flee the burning area (DeBano et al. 1998). Post-fire changes in vegetation structure influence mammal populations for many years. For example, fire in sacaton grasslands was followed by reduced numbers of green vegetation-feeding cotton rats (in response to foliage reduction) and increased numbers of seed-eating pocket mice and kangaroo rats (in response to abundant seed production by annual forbs; Bock and Bock 1978).

Livestock grazing is yet another form of disturbance, the cessation of which (on some reaches of the San Pedro) probably has increased the abundance of those small mammals that require dense vegetation. The substantial increase of plant cover at low height intervals that followed the removal of livestock on the upper San Pedro (Duncan 1988, Krueper et al. 2003) likely has substantially increased the abundance of small mammal species that prefer cover characteristic of grassland or riparian woodland habitats. The increase in herbaceous understory plants may also have increased the number of white-tailed deer (M. Fredlake, personal communication). In contrast, grazing cessation decreased the abundance of small mammal species that prefer more open vegetation structure, such as those characteristic of upland

communities (Boeer and Schmidly 1977, Hayward et al. 1997, Andersen and Nelson 1999). Dense vegetation may also focus medium/large mammal movements onto well-worn paths (C. Hass, personal communication), potentially affecting foraging patterns and species interactions.

Habitat Modification by Mammals

The relationship between habitat and mammal species richness is often viewed as unidirectional, with habitat as the independent variable and species richness as the dependent variable. However, mammals can substantially influence their surroundings. This biotic feedback includes the dam-building activities of beaver, selective foraging by herbivores and granivores, soil disturbance due to burrowing, and seed dispersal.

DAM-BUILDING

Beaver are considered ecological engineers and keystone species in that they have disproportionate effects on ecosystems for their body size and abundance level (Paine 1966, Naiman et al. 1988). Fifteen beaver were released on the upper San Pedro River from 1999 to 2000, resulting in 6 to 12 colonies totaling 50 to 70 beaver, distributed among perennial and intermittent reaches (Snow and Olding 2003, M. Fredlake, personal communication). Preliminary findings on the San Pedro suggest that surface water is increasing in proximity to beaver dams, though there is no information yet on effects of beaver on stream bank vegetation or wildlife (Snow and Olding 2003). Creation of beaver dams in other riparian systems has been found to reduce the slope of the stream channel, reduce streamflow velocity, accelerate sediment deposition, and elevate water tables (Hair et al. 1978, Apple 1985). These changes favor wetland graminoids (grasses and grass-like plants), willows, and other plants that tolerate saturated soils. Beaver further modify vegetation structure by utilizing willow, cottonwood, and seepwillow for food and dam construction and by selectively foraging on aquatic plants such as cattails (Boeer and Schmidly 1977). In response to changes in hydrology and vegetation, species richness of both aquatic and terrestrial avian and mammalian species tends to increase after beaver reintroduction (Hair et al. 1978, Apple 1985). On the San Pedro, beaver activities may increase the abundance of mammals such as the fulvous cotton rat that depend on perennial water or wet meadows, or provide habitat for muskrats should they be reintroduced (Ceballos 1985, Duncan 1988, Ellis et al. 1997).

HERBIVORE AND GRANIVORE FORAGING

Selective foraging by herbivores and/or granivores impacts plant community structure and ecosystem processes (Brown and Heske 1990). For example, the exclusion of kangaroo rats from experimental plots in the Chihuahuan Desert resulted in a threefold increase in tall perennial and annual grasses

(Brown and Heske 1990). Black-tailed prairie dogs may act as a keystone species in semi-arid areas of the Southwest, suppressing competitively dominant woody vegetation such as mesquite (Weltzin et al. 1997). In so doing, the prairie dogs maintain certain areas in a grassland state. Early attempts to eradicate prairie dogs from grazing lands in the San Pedro watershed and other parts of the Southwest (see chap. 11) may have been one of the many factors that contributed to the increased abundance of mesquite and other woody plants in desert grassland habitats (Weltzin et al. 1997).

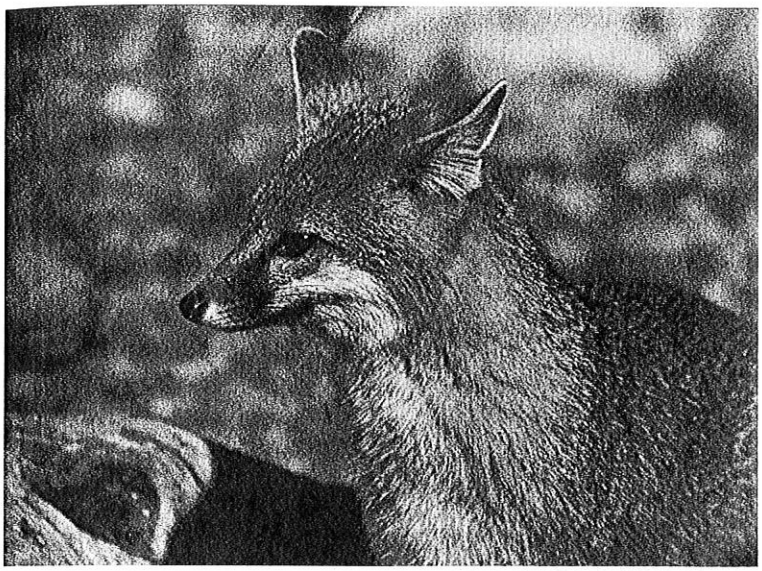
Herbivory by native mammals can be a significant determinant of tree seedling and sapling survivorship in floodplain environments (Andersen and Cooper 2000). Mammals that reduced tree survivorship included beaver, rabbits, and deer. The effects of mammal herbivory were contingent upon flow regime, with trees along regulated rivers declining more than those along unregulated rivers. As a driving mechanism, Andersen and Cooper (2000) suggest that river regulation allows small mammal populations, previously constrained by flooding, to expand in near-river habitats. Long-term monitoring along unregulated rivers such as the San Pedro would be useful to determine whether population size of some mammals increases to high levels during climatic periods characterized by reduced flood magnitude.

SOIL DISTURBANCE

The burrowing activities of small- and medium-sized mammals affect many ecosystem processes and properties. Prairie dogs, such as the black-tailed that once were abundant along the San Pedro, alter nutrient cycling and the rates and pathways of water flow through upland and riparian soils (Weltzin et al. 1997). Similarly, pocket gophers and their kin (still abundant along the San Pedro) fundamentally change physical and biotic processes, making them subterranean ecosystem engineers (Reichman and Seabloom 2002) (fig. 6.1b). By excavating and moving soil, pocket gophers change nitrification and mineralization rates, soil bulk density, and moisture regimes. These activities influence physical and biological processes such as the mixing of soil horizons, soil erosion, plant species richness, and biomass. The burrows and mounds of kangaroo rats have likewise been shown to impact biotic and abiotic habitat properties (Brown and Heske 1990).

SEED DISPERSAL

Mammals are important dispersal agents for numerous plant species and fungi through their consumption and subsequent egestion of seeds and spores and their inadvertent transport of seeds that attach to fur via barbs or hooks (Drezner et al. 2001; and see chap. 4). Rabbits disperse large quantities of seeds in grassland ecosystems with significant effects on the composition and structure of the soil seed bank (Malo and Suarez 1996) and may play a



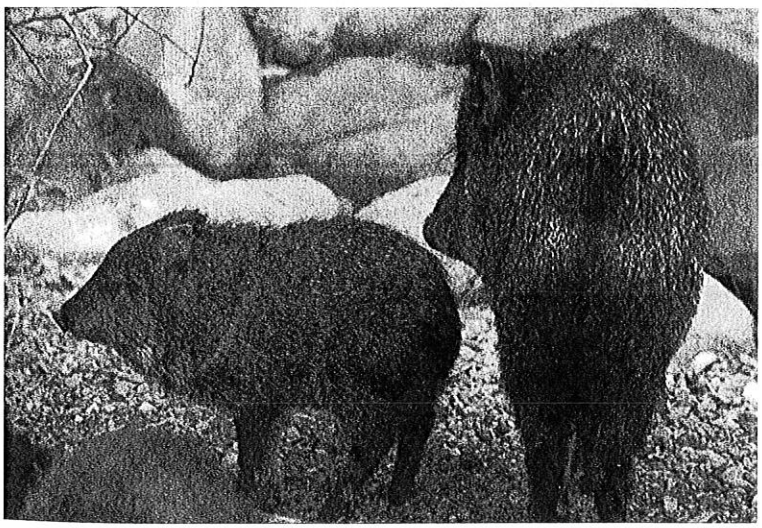


Fig. 6.2. Gray fox (top; 6.2a) and collared peccary (bottom; 6.2b). Photo credits: Robert J. Luce.

similar role in the San Pedro watershed. Seed-caching rodents such as pocket mice, kangaroo rats, and deer mice also disperse seeds (Vander Wall 1997). Along the San Pedro River, mesquite pods and other large seeds, such as hackberry, are consumed or cached by numerous mammals including coyotes, foxes, skunks, peccaries, coati, black bear, and various rodents (Hoffmeister 1986, C. Hass, personal communication, C. Soykan, personal observation) (fig. 6.2). However, the impacts of mammalian seed dispersal for plant and fungal community structure have yet to be studied in this system.

Human Influences

Human activities influence the mammals of the San Pedro watershed both directly (e.g., hunting and road kill) and indirectly (e.g., alteration of hydrologic

regime, land conversion, and other types of habitat modification). Early human impacts on mammals likely were restricted to hunting and habitat modification (agriculture, fire; Wilson 1995). With the arrival of European settlers came further changes in hunting regimes, hydrology, and habitat (Davis 1982, Glennon 2002). Increased hunting and trapping pressure eliminated or reduced the populations of numerous mammals including grizzly bears, gray wolves, and beaver. The loss of top carnivores can have cascading effects on lower trophic levels (Crooks and Soule 1999) but has not been investigated in the San Pedro watershed.

Prairie dogs also once thrived on both sides of the border, but by 1930 only a few remnant colonies could be found in Arizona, although some persist in Sonora. Many ranchers intensely disliked prairie dogs and insisted on their removal because their burrows caused problems for horses and they competed with cattle for grass. As discussed above, the loss of prairie dogs may have contributed to the spread of mesquite into grasslands, altering vegetation structure at the watershed level.

Along with these changes in biota, the San Pedro River went from a wide, slow-flowing series of ciénegas during the 1800s to a narrow, fast-flowing channel bordered by dense forests in the 1900s. Although the role of human actions in this historic river entrenchment is still debated (see chaps. 12 and 13), these changes likely had major impacts on the mammal fauna in the region, with some declining and others benefiting. In particular, mammals associated with marshes and riparian grasslands likely declined, as did those dependent upon upland grassland habitats. Conversely, arboreal species likely benefited from the expansion of the floodplain forests, while adaptable generalists such as deer mice may have benefited from human activities such as irrigated agriculture and ranching (Duncan 1988). Some mammals, such as the collared peccary and Virginia opossum, seem to have expanded their range and increased in abundance in Arizona, possibly as a result of human activities or in response to climate change and associated changes in vegetation (Hoffmeister 1986).

Animals introduced by humans to the San Pedro such as feral dogs, cats, and house mice may affect riparian mammals directly through predation (Hall et al. 2000) or indirectly via competition. Likewise, introduced plant species may affect them both directly, by changing resource availability, or indirectly, by changing vegetation structure (e.g., saltcedar trees grow in denser stands and produce finer litter than do cottonwood and willow trees, thereby influencing small mammal community composition; Ellis et al. 1997). Although few studies have examined the direct or indirect effects of non-native species on mammals along the San Pedro, their impact appears to be minor at this point in time (C. Soykan, personal observation).

More recently, major reaches of the river have been designated as preserves,

and efforts have been undertaken to restore perennial riparian vegetation to abandoned fields, shifting the nature of human impacts. Road kill may have replaced hunting as the primary source of mortality for medium and large mammals along the river. Although no data exist for the San Pedro, a nearby study conducted in Saguaro National Park East suggests that thousands of mammals die annually due to road kill (Kline and Swann 2001).

Outside of protected areas, urban sprawl has altered habitat and increased human-wildlife conflicts (McKinney 2002). Urban and suburban sprawl threaten to intersect wildlife corridors that connect the river with protected lands in the surrounding mountains (Hass 2001). The river, its tributaries, and washes form important movement corridors for mammal species, providing cover, food, water, and easy passage through less-hospitable desert scrub habitats. By disconnecting the river from its tributaries or fragmenting reaches along the river, sprawl may reduce movement among suitable habitat patches, resulting in increased risk of local extinction due to reduced potential for recolonization. Furthermore, reduced movement opportunities would impede the natural recolonization of the watershed by extirpated species such as otter and jaguar that have source populations nearby.

Human population growth and associated water use has already altered stream hydrology (see chap. 15). If present trends continue, increasing portions of the river will cease to flow permanently, resulting in a loss of surface water—a vital resource for many of the mammal species that live in the region. Declining water tables would also alter riparian vegetation structure, with effects on mammal communities. At the same time, some portions of the river (including portions of the lower basin; see chap. 19) are expected to gain perennial streamflow, potentially offsetting the loss of water and riparian habitat elsewhere. However, the lower basin reaches are more arid than those of the upper basin, with less rain falling during the hot summer months. Longitudinal (upstream-downstream) studies of mammal abundance, as well as comparisons of mammal abundance between reaches with perennial vs. intermittent streamflow, would be valuable in helping us to understand how mammal populations may change over time along the San Pedro River in response to changes in stream hydrology.

Summary and Conclusion

The high mammal species richness of the San Pedro watershed can be attributed to a variety of factors including biogeographic position, climate, water availability, primary productivity, vegetation composition, structure, and heterogeneity, disturbance regimes, and species interactions. For simplicity, we have grouped these factors together into three categories—Geography, Environmental Gradients, and Non-equilibrium Processes—and discussed them using specific examples. Overall, existing data support our hypotheses,

but much work remains to be done. Future efforts should focus on the specific mechanism(s) responsible for generating and/or maintaining species richness patterns. A fruitful approach may involve comparing species richness gradients from riparian to upland habitats, as suggested by Sabo et al. (2005). A hierarchical perspective of species richness may provide another useful method, bringing together mechanisms that operate at different spatio-temporal scales into a single predictive model (Sarr et al. 2005).

Just as habitat characteristics influence mammal communities, so too do mammals influence the habitats in which they live. Dam building by beavers and burrowing by rodents represent ecosystem engineering activities that significantly alter the physical and biological attributes of a habitat. Likewise, selective foraging by herbivores and granivores and seed dispersal can have important impacts on plant communities. Nevertheless, humans have had a far greater impact on the San Pedro watershed and its biota than any other mammal. Activities such as hunting, agriculture, and grazing were the first wave of human impacts, but these have been replaced by groundwater pumping and urbanization, which together represent the greatest, and most permanent, current threats to the mammals of the San Pedro. If left unchecked, groundwater pumping will lower water tables, leading to a loss of environmental gradients, while urbanization will isolate the watershed from surrounding regions. A reduction or loss of two out of the three factors hypothesized to account for the San Pedro's high mammal species richness would provide an interesting, albeit somber, test of our ideas. Ultimately, anthropogenic disturbance may prove to be the most important factor influencing mammal species richness along the San Pedro.