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NEW INFORMATION ON THE LATE PLEISTOCENE BIRDS FROM SAN JOSECITO CAVE, NUEVO LEÓN, MEXICO[1]

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Abstract. We report 90 bird bones representing 18 species from recent excavations at San Josecito Cave, Nuevo León, Mexico. The new material increases the avifauna of this rich late Pleistocene locality from 52 to 62 species. Eight of the 10 newly recorded taxa are extant; each is either of temperate rather than tropical affinities (such as the American Woodcock *Scolopax minor* and Pinyon Jay *Gymnorhinus cyanocephalus*) or is very widespread in its modern distribution. The two extinct taxa are a stork (*Ciconia* sp. or *Mycteria* sp.) and *Geococcyx californianus conklingi*, a large temporal subspecies of the Greater Roadrunner. In this region of the Sierra Madre Oriental (about lat. 24°N, long. 100°W, elev. 2,000–2,600 m), the late Pleistocene avifauna was a mixture of species that today prefer coniferous or pine-oak forests/woodlands, grasslands/savannas, and wetlands. As with various late Pleistocene plant and mammal communities of the United States and México, no clear modern analog exists for the late Pleistocene avifauna of San Josecito Cave.

Key words: Late Pleistocene avifaunas; Mexico; historical biogeography; extinct species; temperate/tropical transition.

INTRODUCTION

San Josecito Cave is located on a steep western flank of the Sierra Madre Oriental, southern Nuevo León, Mexico (lat. 23°57′21″N, long. 99°54′45″W, elev. about 2,250 m; Fig. 1). The site lies in the Municipio de General Zaragoza, about 1 km SSW of Ejido San Josecito and 8 km SW of Aramberri. The primary vegetation type within a 2 km radius of the cave is pine-oak forest and woodland, classified as "montane mesic forest" (Muller 1939), which is the eastern equivalent of "Madrean evergreen woodland" in the Sierra Madre Occidental (Brown 1982). Within the 2 km radius, which would accomodate the primary home range of most vertebrate species whose bones have accumulated in the cave, the elevation varies from 2,000 to 2,600 m. Only about 20 km south of San Josecito Cave is Cerro Peña Nevada, at 3,650 m one of the tallest peaks in the Sierra Madre Oriental.

During four trips in 1988–1990, research teams from Mexico and the United States began a program of carefully evaluating, mapping, and

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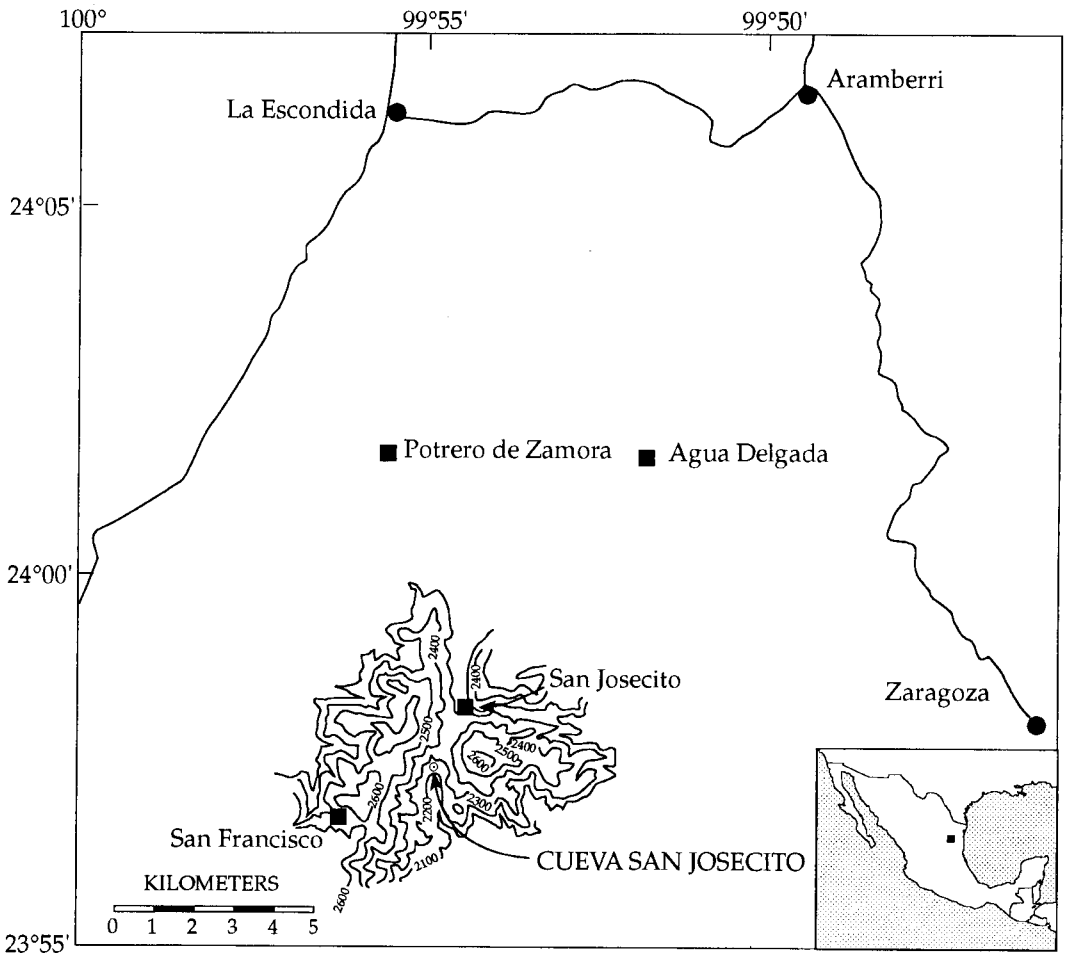

FIGURE 1. The location of San Josecito Cave, Sierra Madre Oriental, Nuevo León, México, in relation to local *ejidos* (squares) and towns (circles).

excavating the fossiliferous sediments of San Josecito Cave (Arroyo-Cabrales 1991; Arroyo-Cabrales and Johnson, in press; Arroyo-Cabrales et al. 1989, 1993). Their goal was to improve the understanding of the stratigraphy, chronology, and taphonomy of San Josecito Cave's important late Pleistocene vertebrate fauna, which had been known previously only from material excavated under the direction of Chester Stock, California Institute of Technology, from 1935 to 1941 (Stock 1943).

San Josecito Cave is developed in folded Late Jurassic or Early Cretaceous limestone. It is a single-drop fissure with three natural entrances that descend vertically 12 to 30 m to a single main room that is 34 m long by 25 m wide. No horizontal or walk-in entrances exist today. Even while bones were accumulating in the late Pleistocene, it seems likely that vertical entrances provided the only access to the cave.

Stock and his crew excavated and removed fossiliferous sediments to an average depth of about 12 m below the original sediment surface of the cave. They recovered about 100,000 bones, now housed in the Natural History Museum of Los Angeles County (LACM), California.

Approximately 108 species of late Pleistocene vertebrates are known from San Josecito Cave (Arroyo-Cabrales and Johnson, in press). Stock's original excavations yielded bones of these 19 species of extinct mammals characteristic of the late Pleistocene: the bats *Desmodus stocki, Plecotus tetralophodon,* ground sloths *Megalonyx* sp., *Nothrotheriops shastensis,* rabbit *Sylvilagus leo-*

nensis, pocket gopher *Orthogeomys onerosus,* canids *Canis dirus, Cuon alpinus,* bear *Tremarctos floridanus,* cats *Felis atrox, Smilodon fatalis,* horse *Equus alaskae,* peccary *Platygonus* sp., camel *Camelops* sp., cervids *Navahoceros fricki, Odocoileus* sp., pronghorn *Stockoceros conklingi,* and bovids *Euceratherium* sp., *Oreamnos* cf. *O. harringtoni.* Among the 10 species of mammals identified thus far from the new excavation are three extinct species: *Desmodus stocki, Nothrotheriops shastensis,* and *Equus alaskae* (Arroyo-Cabrales et al. 1993).

L. Miller (1943) reported 43 species of birds from Stock's excavations. Subsequent examination of the 2,100+ bird bones available to Miller has increased the San Josecito Cave avifauna to 52 species (Howard 1971; Olson 1974, 1984; Arroyo-Cabrales and Johnson, in press; see Table 1 herein), dominated by scavengers (teratorns, vultures, ravens, certain hawks and falcons) and predators (owls, certain hawks and falcons).

MATERIALS AND METHODS

The new excavations consist of a 1.0 × 0.3 m unit (designated 533N 197E; thickness 1.26 m), a 0.5 × 0.5 m unit (534N 197E; thickness 0.42 m), and a 0.3 × 0.4 m unit (542N 196E; thickness 0.23 m). The first two units are stratigraphically equivalent to the deepest sediments excavated by Stock, based on *in situ* correlations with Stock's system of vertical control (marks chiseled on the cave's wall), supplemented by his field correspondence and photographs (Arroyo-Cabrales et al. 1993). Unit 542N 196E corresponds to the uppermost strata from the cave's original sediment surface, 12 m above the other two units.

The radiocarbon chronology of the San Josecito Cave bone deposit is only partially understood. Humate-based radiocarbon dates suggest that units 533N 197E and 534N 197E are about 27,000 to 45,000 years B.P., while unit 542N 196E is latest Pleistocene, most likely between about 11,000 and 27,000 years B.P. (Arroyo-Cabrales et al., unpubl. data).

Identification of avian fossils (by DWS) is based on comparisons with modern skeletal specimens in the collections of the New York State Museum (NYSM) and the National Museum of Natural History, Smithsonian Institution (USNM). The recently excavated bones from San Josecito Cave are catalogued in the collections of the Laboratorio de Paleozoología, Instituto Nacional de Antropología e Historia (INAH), Mexico City (Arroyo-Cabrales and Polaco 1992).

Unless cited otherwise, the information on generalized modern distributions of Mexican birds is from Friedmann et al. (1950), Blake (1953), A. Miller et al. (1957), Peterson and Chalif (1973), AOU (1983), and A. Phillips (1986). We have found no studies of modern birds within 50 km of San Josecito Cave. Birds from various elevations and habitats within 175 km of the site have been reported by J. Phillips (1911), Sutton and Burleigh (1939), Burleigh and Lowery (1942), Sutton and Pettingill (1942, 1943), Moore (1947), Eaton and Edwards (1948), Sutton et al. (1950), Robins and Heed (1951), Van Hoose (1955), Packard (1957), Zimmerman (1957), Martin del Campo (1959), Ely (1962), Contreras-Balderas (1973, 1978, 1988, 1992), and F. Webster (1974). While each of these papers helps to interpret the biogeography and paleoecology of the San Josecito Cave avifauna, the five described in the next paragraph are most pertinent because of similarities in habitat and elevation.

From 12 to 25 April 1941, the field party of Burleigh and Lowery (1942) studied birds in the pinyon-juniper-oak woodlands at Diamante Pass, Zapalinamé Mountain, Sierra Guadalupe, southeastern Coahuila (elev. about 2,100–3,000 m, lat. 25°20′N, long. 100°55′W, about 175 km NNW of San Josecito Cave). This region had been visited briefly (6 March 1938) by Sutton and Burleigh (1939). Ely (1962) also studied birds in this region at various times from 24 December 1957 to 13 June 1959, covering a broader geographic and altitudinal range. As summarized by Sutton and Pettingill (1943), Robert B. Lea and Dwain W. Warner recorded birds from 7 to 14 March 1941 near Galeana, southern Nuevo León (elev. about 2,000–2,500 m, lat. 24°50′N, long. 100°05′W, about 100 km NNW of San Josecito Cave). Also near Galeana, Contreras-Balderas (1992) studied birds in a pine-juniper-creosotebush community (*Pinus ponderosa-Juniperus monosperma-Larrea tridentata*) at 2,100 m elev., lat. 24°41′N, long. 100°12′W (about 80 km NNW of San Josecito Cave) and a creosotebush-yucca community (*Larrea tridentata-Yucca filifera*) at 1,990 m elev., lat. 24°43′N, long. 100°14′W (about 85 km NNW of San Josecito Cave.

RESULTS

Of the 90 bird bones from the new excavations that can be identified at least to the ordinal level

(Table 1), 73 are from unit 542N 196E, 16 are from 534N 197E, and one is from 533N 197E. The 39 specimens identified to genus or species represent 18 species of birds (12 non-passerines, six passerines), among which are 32 bones from unit 542N 196E, six from 534N 197E, and one from 533N 197E. The species compositions of these three sub-assemblages may be similar, although this cannot be determined with such small samples. The use of fine-mesh screen is reflected in the dramatically improved recovery of non-*Corvus* passerine bones, which make up 67% (60 of 90) of the bones in our sample, contrasting with the "very few" non-*Corvus* passerine bones mentioned but not identified by L. Miller (1943). Fifty-one of the 60 passerine bones are from small to medium-sized species that are very difficult to identify.

The two most numerous species in our sample, *Asio otus* and *Cyrtonyx montezumae,* were also common among the 2,100+ bird bones from San Josecito Cave studied by L. Miller (1943). Both of these species are recorded regularly in late Pleistocene cave assemblages (Mead et al. 1984). Remarkably, however, 10 of the 18 species in our sample are not among those identified by L. Miller (1943). Furthermore, our sample does not include many of the most common species in the original faunal assemblage, such as *Coragyps atratus, Aquila chrysaetos, Caracara plancus, Falco mexicanus,* the peculiar extinct turkey *Meleagris crassipes* (see Rea 1980, Steadman 1980), *Tyto alba, Bubo virginianus,* or *Strix occidentalis. Corvus corax* represented more than half the bones reported by L. Miller (1943), but only a single bone in our sample. The absence or scarcity of these species in our sample may be an artifact of small sample size, or it may reflect a genuine faunal change related to differences in taphonomy (how the cave was sampling birds) or chronology (potential changes in climate and vegetation). Further excavation will test these proposals.

Certain modern species of birds are excellent indicators of habitat today, and as such are important in reconstructing late Quaternary habitats. At least 26 species of birds from San Josecito Cave inhabit pine-oak forests or woodlands of Mexico or southwestern United States today (category MW in Table 1). Of these, 13 species were recorded from southeastern Coahuila by Burleigh and Lowery (1942) and Ely (1962). Near Galeana, Nuevo León, 12 of the 26 MW species were recorded by Sutton and Pettingill (1943) or Contreras-Balderas (1992).

Grassland species make up another very strong component (24 species, including 14 listed as well in another habitat category). Especially good indicators of grassland are *Buteo* cf. *B. regalis, Circus cyaneus, Numenius* cf. *N. americanus, Burhinus* cf. *B. bistriatus, Asio flammeus,* and *Sturnella* sp. These species, however, do not necessarily suggest treeless prairies. They also may occur in grassy areas with scattered trees or shrubs, such as alpine savannahs, open pine-oak woodlands, sagebrush steppe, or even grassy desert-scrub such as occurs today in much of the Chihuahuan Desert. Of San Josecito Cave's 24 "grassland" species, 12 were recorded from southeastern Coahuila (Burleigh and Lowery 1942, Ely 1962) and six from near Galeana, Nuevo León (Sutton and Pettingill 1943, Contreras-Balderas 1992).

The San Josecito Cave assemblage also includes 12 wetland species (grebe, heron, four ducks, three rails, three shorebirds). Except for a few small perennial streams, wetlands are absent in the mountainous terrain near San Josecito Cave today. None of the 12 wetland species was recorded by Burleigh and Lowery (1942), whereas Sutton and Pettingill (1943) and Contreras-Balderas (1992) noted only two of them.

There are no previous modern or prehistoric records in Mexico for the American Woodcock *Scolopax minor.* The modern winter and breeding ranges of *S. minor* do not extend south of Texas (AOU 1983), about 500 km and 800 km, respectively, northeast of southern Nuevo León. The preferred habitats of *S. minor,* whether nesting or wintering, are moist woodlands with good soil cover or brushy swamps.

Within Mexico, the Pinyon Jay *Gymnorhinus cyanocephalus* breeds only in the mountains of northern Baja California, with occasional non-breeding records for the northern Sierra Madre Occidental in Sonora and Chihuahua (Moore 1951, Selander 1956). The nearest resident populations are in the mountains of south-central New Mexico, about 1,000 km NW of southern Nuevo León. The occurrence of *G. cyanocephalus* at San Josecito Cave undoubtedly is related to the expansion of coniferous woodlands (especially pinyon-juniper) in northern Mexico during the late Pleistocene (Van Devender 1990).

Within Nuevo León, the Scrub Jay *Aphelocoma coerulescens* (= *A. californica* of A. Phillips

TABLE 1. Birds from San Josecito Cave, Nuevo León, Mexico. The identification and nomenclature of certain taxa reported by L. Miller (1943) for the original excavations are modified according to Howard (1971), Olson (1974, 1984), AOU (1983), Arroyo-Cabrales and Johnson (in press), specimen labels in LACM, and herein. The status of some other taxa reported by L. Miller (1943) may change with further study. Bones from unit 542N are similar in age to those from Stock's original excavations (11,000 to 27,000 years B.P.), while those from units 533N and 534N are 27,000 to 45,000 years B.P.

Numbers are NISP (number of identified specimens). # = NISP in LACM collections unreported. Bone element categories for the 1990 excavations: c = carpometacarpus, co = coracoid, f = femur, fu = furcula, h = humerus, m = mandible, mp = manus phalanx, p = pedal phalanx, r = radius, ro = rostrum, s = scapula, t = tarsometatarsus, ti = tibiotarsus, u = ulna, v = vertebra.

* = extinct species. + = recorded at Diamante Pass, southeastern Coahuila, by Sutton and Burleigh (1939), Burleigh and Lowery (1942) or Ely (1962). & = recorded near Galeana, southern Nuevo León, by Sutton and Petingill (1943) and/or Contreras-Balderas (1992).

Distribution categories: MT = mostly tropical (current range is mostly south of 28°N and entirely south of 40°N); TE = temperate (most of current range is north of 28°N); TR = tropical (current range is south of 28°N); WI = widespread (both temperate and tropical).

Habitat categories (very generalized): G = grassland or grassy savannah; MW = montane woodland or forest (dominated by some combination of oak, pines, juniper, other conifers); TF = tropical forest; WE = wetland. Distribution and habitat are not designated for most extinct species because of the paucity of late Pleistocene records south of San Josecito Cave.

Taxon	Original excavations	1990 Excavations		Distribution	Habitat
		542N	533N 534N		
Podicipedidae					
+*Podilymbus podiceps* Pied-billed Grebe	#	—	—	WI	WE
Ardeidae					
Nycticorax nycticorax Black-crowned Night-Heron	1	—	—	WI	WE
Anatidae					
Aix cf. *A. sponsa* Wood Duck	#	—	—	TE	WE
Anas sp. dabbling duck	#	—	—	WI	WE
cf. *Histrionicus* sp. ?Harlequin Duck	"a few"	—	—	TE	WE
&*Oxyura* cf. *O. jamaicensis* Ruddy Duck	#	—	—	WI	WE
Ciconiidae					
**Ciconia* sp. or *Mycteria* sp. stork	—	1 ra	—	—	—
Teratornithidae					
**Teratornis merriami* Merriam's Teratorn	15	—	—	—	—
Vulturidae					
Gymnogyps californianus California Condor	12+	—	—	TE	G,MW
+*Coragyps atratus* Black Vulture	"lots"	—	—	—	—
Accipitridae					
Elanus leucurus White-tailed Kite	1	—	—	MT	G
+*Parabuteo unicinctus* Harris' Hawk	±20	—	—	MT	G
Buteo nitidus Gray Hawk	#	—	—	MT	MW
Buteo cf. *B. regalis* Ferruginous Hawk	#	—	—	TE	G

TABLE 1. Continued.

Taxon	Original excavations	1990 Excavations 542N	1990 Excavations 533N 534N	Distribution	Habitat
+&*Buteo jamaicensis* Red-tailed Hawk	—	1 mp	—	WI	G,MW
+*Aquila chrysaetos* Golden Eagle	±75	—	—	TE	G
**Spizaetus grinnelli* Grinnell's Eagle	2	—	—	—	—
**Wetmoregyps daggetti* Daggett's Eagle	3	—	—	—	—
**Neogyps errans* Large accipitrid vulture	7	—	—	—	—
**Neophrontops americanus* Small accipitrid vulture	27	—	—	—	—
+*Circus cyaneus* Northern Harrier	4	—	—	WI	G
Falconidae					
Caracara plancus Crested Caracara	"fairly abundant"	—	—	—	—
+&*Falco mexicanus* Prairie Falcon	40	—	—	TE	G
+&*Falco sparverius* American Kestrel	17	3 c,t,ti	—	WI	G
Falco sp. falcon	#	—	—	—	—
Phasianidae					
+*Cyrtonyx montezumae* Montezuma Quail	80	3 2h,c	2 c,p	MT	MW
Dendrortyx (?) sp. Wood-Quail	2	—	—	TR	MW
**Meleagris crassipes* Great-footed Turkey	90	—	—	—	—
Rallidae					
Rallus limicola Virginia Rail	—	1 t	1 t	WI	WE
Rallus elegans/longirostris King/Clapper Rail	1	—	—	—	WE
+&*Fulica americana* American Coot	2	—	—	WI	WE
Charadriidae					
Pluvialis sp. plover	#	—	—	WI	G,WE
Scolopacidae					
Scolopax minor American Woodcock	—	2 c,ti	—	TE	G,WE
Numenius cf. *N. americanus* Long-billed Curlew	1	—	—	WI	G,WE
Burhinidae					
Burhinus cf. *B. bistriatus* Double-striped Thick-Knee	1	—	—	TR	G
Columbidae					
+&*Columba fasciata* Band-tailed Pigeon	9	1 t	—	WI	MW
+&*Zenaida macroura* Mourning Dove	3	—	—	WI	G,MW

TABLE 1. Continued.

Taxon	Original excavations	1990 Excavations 542N	1990 Excavations 533N 534N	Distribution	Habitat
Psittacidae					
Rhynchopsitta pachyrhyncha Thick-billed Parrot	9	—	—	MT	MW
+*Rhynchopsitta* cf. *R. terrisi* Maroon-fronted Parrot	#	—	—	TR	MW
Cuculidae					
+**Geococcyx californianus conklingi* Conkling's Greater Roadrunner	±40	1 h	—	—	—
Tytonidae					
Tyto alba Common Barn-Owl	95	—	—	WI	G,MW
Strigidae					
+*Otus asio/kennicotti* Eastern/Western Screech-Owl	3	3 h,p,t	1 co	WI	G,MW
+*Otus flammeolus* Flammulated Screech-Owl	12	—	—	WI	MW
Otus trichopsis Whiskered Screech-Owl	6	—	—	MT	MW
+*Bubo virginianus* Great Horned Owl	"several hundred"	—	—	WI	G,MW
**Bubo* sp. Large owl	1	—	—	—	—
+*Glaucidium gnoma (?)* Northern Pygmy-Owl	2	—	—	WI	MW
Micrathene cf. *W. whitneyi* Elf Owl	#	—	—	MT	G,MW
Strix occidentalis Spotted Owl	43	—	—	WI	MW
Aegolius acadicus Northern Saw-whet Owl	9	—	—	WI	MW
Asio otus Long-eared Owl	±100	6 3c,2p,u	1 v	TE	MW
Asio flammeus Short-eared Owl	—	1 u	—	WI	G
Ciccaba virgata Mottled Owl	±20	—	—	TR	TF
Caprimulgidae					
+*Phalaenoptilus nuttallii* Common Poorwill	1	1 h	—	WI	G,MW
Picidae					
+&*Colaptes auratus* Northern (Red-shafted?) Flicker	?	—	—	WI	G,MW
Hirundinidae					
+*Hirundo pyrrhonotus* Cliff Swallow	—	2 juv h,t	—	WI	G,MW
Corvidae					
Gymnorhinus cyanocephalus Pinyon Jay	—	—	1 h	TE	MW
+*Aphelocoma coerulescens* Scrub Jay	—	1 t	—	WI	MW
+*Corvus corax* Common Raven	"more than ½ the bones"	1 juv ti	—	WI	G,MW

TABLE 1. Continued.

Taxon	Original excavations	1990 Excavations 542N	1990 Excavations 533N 534N	Distribution	Habitat
Muscicapidae					
+*Turdus migratorius* American Robin	—	2 mp,t	—	WI	MW
Icteridae					
+&*Sturnella* sp. meadowlark	—	2 p,ti	1 ti	WI	G
Passeriformes Small-medium passerines	"very few"	41 misc	10 misc	—	—
Totals	2,100+	73	17	7 MT 9 TE 4 TR 28 WI	24 G 26 MW 1 TF 12 WE

1986:46) occurs only in the mountains of the westernmost part of the state, and "possibly very locally elsewhere, *fide* J. T. Marshall" (A. Phillips 1986:48). The late Pleistocene range of *A. coerulescens* probably was less disjunct than it is today, again because of the greatly expanded extent of pinyon-juniper woodlands.

Unless bones of juveniles are recovered, such as for the Cliff Swallow *Hirundo pyrrhonotus* and Common Raven *Corvus corax,* it is difficult to establish whether the bones of any particular migratory species represent breeding versus nonbreeding populations. Larger samples may resolve this problem eventually in species such as the American Robin *Turdus migratorius,* for which both resident and migratory populations exist in the region (J. Webster 1959). While we were unable to identify the single bone of *Sturnella* to species, the breeding form in southern Nuevo León today is the Western Meadowlark *S. neglecta* rather than the Eastern Meadowlark *S. magna* (Lanyon 1962).

All but two of the 18 species in the new faunal sample are extant. The first extinct taxon is an undetermined stork (*Ciconia* sp. or *Mycteria* sp.), represented by the distal end of a radius that is smaller than in any extant or extinct New World species of stork. It is also less pneumatic than in *Jabiru.* Compared to the radius from four species each of *Ciconia* and *Mycteria,* the San Josecito Cave specimen has a broader (relative to total width of distal end) sulcus tendineus. It is most similar in size and qualitative characters to the radius in *Ciconia episcopus microscelis* (female from Zimbabwe, USNM 431493) and *Mycteria ibis* (female from Tanzania, USNM 488125). As noted by Olson (1991), the North American late Pleistocene record of storks still does not include any living species. Modern New World storks prefer low elevation wetlands. The radius from San Josecito Cave is the highest elevational record, past or present, for any stork from North or Central America. A carrion-feeding association with extinct megafauna, much as still occurs in parts of Africa today, may account for the greater late Pleistocene range of North American storks and other avian scavengers (Steadman and Martin 1984, Steadman and Miller 1987).

The second extinct taxon in the new faunal sample is *Geococcyx californianus conklingi,* represented by the distal half of a humerus. The width of this specimen (11.4 mm) resembles that in two late Pleistocene specimens of *G. c. conklingi* (11.2, 11.7 mm) from Conkling Cavern and Shelter Cave, New Mexico (Harris and Crews 1983). These measurements are larger than in the living Greater Roadrunner *G. c. californianus* (8.8–10.6 mm, $n = 26$; Harris and Crews 1983). The Lesser Roadrunner *G. velox* of western and southern Mexico is even smaller than *G. c. californianus. Geococcyx conklingi* was described as an extinct full species by Howard (1931) from Conkling Cavern. It is not known outside of southern New Mexico and San Josecito Cave. Harris and Crews (1983) regard *G. c. conklingi* as a large geographic and temporal subspecies of

the living *G. c. californianus*, the larger size being the result of adaptation to the cooler summers of the late Pleistocene. If this is so, then *G. californianus conklingi* probably is ancestral to *G. c. californianus*.

The same situation is true for at least two other species from San Josecito Cave for which "extinct" temporal forms ("chronospecies") have been described. Pleistocene specimens of the Black Vulture *Coragyps atratus* often are referred to as *C. occidentalis* or *C. o. mexicanus* (see Brodkorb 1964:254, Howard 1968, Steadman and Martin 1984). Similarly, Pleistocene bones of the Crested Caracara (*Polyborus plancus* of AOU 1983; *Caracara plancus* of Banks and Dove 1992) have been referred to as *P. prelutosus* or *P. prelutosus grinnelli* (but see Olson 1976). For neither the Black Vulture or Crested Caracara is there any evidence that the Pleistocene form is not ancestral to the living species, forming an evolutionary continuum.

DISCUSSION AND CONCLUSIONS

The San Josecito Cave avifauna now consists of at least 62 species, the richest late Pleistocene assemblage from Mexico. That only 39 newly identified bones would include 10 species previously unrecorded from the site shows that we are nowhere near reaching the point of diminishing returns in sampling the San Josecito Cave avifauna. Further excavations are sure to disclose additional species. Five of the newly added species are passerines (Cliff Swallow, Pinyon Jay, Scrub Jay, American Robin, meadowlark sp.). As a larger bone sample becomes available, a thorough attempt to identify a significant portion of the small to medium-sized passerine bones will be essential to compare the past and present avifaunas of the San Josecito region more precisely. Although unsurveyed, the modern avifauna undoubtedly is dominated by passerines. The only extinct fossil passerine known thus far from highland Mexico is a bunting (cf. *Passerina*) from the late Pliocene Yepómera fauna in Chihuahua (Steadman and McKitrick 1982).

Another aspect of future research is to re-examine the material collected by Stock, some of which has not been studied for 50 years. Among the unresolved taxonomic and osteological problems are the *Rhynchopsitta* parrots, two species of which have been reported from San Josecito Cave. Only one species (*R. terrisi*) occurs in this region today (Moore 1947), although some authors (e.g., Hardy and Dickerman 1955) would synonymize *R. terrisi* with *R. pachyrhyncha* of the Sierra Madre Occidental. Burleigh and Lowery (1942) reported *R. pachyrhyncha* from Diamante Pass, Coahuila. These birds were, in fact, *R. terrisi*, which had not yet been described.

Much of the late Pleistocene extinction of North American birds has been related to dependencies (especially carrion feeding) on the vast large mammal fauna, most species of which died out about 12,000 to 10,000 years ago (Martin 1984, Steadman and Martin 1984, Steadman and Miller 1987). Even if we discount the various extinct species of birds, no exact modern analog exists for the late Pleistocene avifauna of San Josecito Cave. In other words, there is no place in Mexico or the United States today where, within a radius of several kilometers, one could find the same assemblage of forest/woodland, grassland, and wetland species.

In recording species that are allopatric today, the San Josecito Cave avifauna resembles the many North American late Pleistocene mammalian "disharmonious faunas." Each of these faunas consists of species of small mammals that today occur hundreds of kilometers in different directions from the fossil site in question (Lundelius et al. 1983; Semken 1984, 1988; Graham 1985; Stafford and Semken 1990). The area that most closely represents a modern analog for a disharmonious fauna, even though it may not include all mammalian species in the late Pleistocene assemblage, is generally to the north or northwest of the fossil site. At San Josecito Cave, however, it is impossible at present to demonstrate contemporaneity of taxa. Because so much time is represented, the San Josecito Cave avifauna is not homologous to a modern species assemblage. Rather, the San Josecito Cave avifauna is a time-transgressive series of small samples of local birds. The new excavations, which feature temperate or widespread species rather than tropical taxa, are a first step toward addressing this problem.

The eastern slopes of the Sierra Madre Oriental are generally wetter, less seasonal in rainfall and temperature, more heavily forested, and support a more tropical biota than the western slopes. This difference may be part of the reason why tropical species are poorly represented at San Josecito Cave. One of these tropical species,

the Mottled Owl *Ciccaba virgata,* occurs today only at lower elevations at the latitude (23°57′) of San Josecito Cave. To the south, however, at lat. 21°25′ in San Luis Potosí, *C. virgata* has been recorded in pine-oak forest at 1,500 to 2,100 m elevation (Davis 1952).

Much remains to be learned about the historical vertebrate biogeography of the Sierra Madre Oriental, the adjacent coastal lowlands to the east, and the Chihuahuan desert to the west. As elsewhere in Mexico (Brown 1985), this region was profoundly influenced by late Quaternary changes in climate and vegetation (Martin et al. 1954; Martin 1955, 1958; Martin and Harrell 1957; Bryant and Riskind 1980). Glacial climates, as opposed to the warm interglacial climates of the past 10,000 years, have been operative for about 85–90% of the past 250,000 years (Dansgaard et al. 1993). Late glacial climates averaged 4–5°C cooler than today virtually throughout the Neotropics, whereas the associated moisture regimes were much more variable (Markgraf 1989, Lozano-García et al. 1993). In the Chihuahuan Desert of Mexico, a cooler and perhaps moister late Pleistocene climate led to the development of vast wetlands in areas unable to sustain such wetlands during the warmer Holocene climates of the past 10,000 years (Meyer 1973, Van Devender 1990). By contrast, evidence from more southern parts of highland Mexico suggests that glacial times averaged drier than the Holocene (Watts and Bradbury 1982, Lozano-García et al. 1993).

Areas of northern Mexico now covered with Chihuahuan desertscrub were occupied until about 10,000 years ago by a pinyon-juniper woodland (Van Devender 1990). Just as with birds or mammals, the late Pleistocene plant assemblages were "disharmonious" because independent geographic responses of individual species produced plant communities without exact modern analogs (Van Devender 1990). Plants characteristic of higher elevation communities (stunted spruce-pine forests, alpine tundra; see McDonald 1990) also were depressed in elevation as much as 1,000 m lower than at present (McDonald 1993). Under this cooler than modern climatic regime, true alpine conditions may have extended from the high elevation region of Sierra Peña Nevada (elev. 3,000–3,650 m) to the area around San Josecito Cave (elev. 2,100–2,600 m). Proximity to an alpine environment might account for the strong temperate component in the San Josecito Cave avifauna. The cave also has yielded bones of the yellow-bellied marmot (*Marmota flaviventris*), an alpine sciurid that today lives only north of Mexico (Frase and Hoffmann 1980; Arroyo-Cabrales and Johnson, in press).

At Rancho la Brisca, in the western foothills of the Sierra Madre Occidental in northern Sonora (lat. 30°23′, long. 110°33′, elev. 1,000 m), Van Devender et al. (1985) hypothesized that the vertebrate fauna during the Sangamon interglacial (about 125,000 years ago; Clark 1992) was even more tropical than that existing today, with the best modern analog at lower elevations about 240 km to the south-southeast. The deep deposits in San Josecito Cave, thus far representing only the last glacial interval, eventually may be found to sample the previous interglacial, thereby providing data on the waxing and waning of temperate versus tropical components in the vertebrate communities of northeastern Mexico.

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