

## TWO NEW LATE PLEISTOCENE AVIFAUNAS FROM NEW MEXICO

REBECCA L. BRASSO AND STEVEN D. EMSLIE<sup>1</sup>

Department of Biology and Marine Biology, University of North Carolina, 601 S. College Road,  
Wilmington, NC 28403

**Abstract.** We report two new late Pleistocene avifaunas from New Mexico, recovered from Sandia Cave during archaeological excavations by F. Hibben in the 1930s and the nearby Marmot Cave excavated in 2000. The fossil assemblage from Sandia Cave consists of at least 30 taxa, including seven extralimital and two extinct species, *Coragyps occidentalis* (extinct vulture) and *Ectopistes migratorius* (Passenger Pigeon). The avifauna from Marmot Cave is limited to eight taxa shared with Sandia Cave. Two new records of *Gymnogyps californianus* (California Condor) are reported from these sites, as well as new records of *Lagopus* sp. (ptarmigan), *Aegolius funereus* (Boreal Owl), and *Micrathene whitneyi* (Elf Owl) from New Mexico. Two new radiocarbon dates on fossil *G. californianus* from Sandia and Marmot cave are reported at  $10\,795 \pm 50$  and  $25\,090 \pm 220$  <sup>14</sup>C years before present (B.P.), respectively. These collections provide further evidence for mixed avian communities in New Mexico during the late Pleistocene and are similar to other cave avifaunas of comparable age from the Great Basin and Rocky Mountain regions. The birds from Sandia Cave that are shared with other fossil avifaunas include species currently found in arctic tundra, boreal, and steppe habitats, as well as open, xeric communities. This collection provides additional evidence for widespread steppe-tundra, shrub, and subalpine forest environments at lower elevations of western North America during the late Pleistocene.

**Key words:** fossil avifauna, late Pleistocene, Marmot Cave, New Mexico, Sandia Cave.

## Dos Avifaunas del Pleistoceno Tardío de Nuevo México

**Resumen.** Se reportan dos nuevas avifaunas del Pleistoceno tardío de Nuevo México, encontradas en Cueva Sandía durante excavaciones arqueológicas dirigidas por F. Hibben en la década de 1930 y en Cueva Marmota durante excavaciones realizadas en el año 2000. La asamblea fósil de Cueva Sandía consiste de al menos 30 taxa, incluyendo siete

especies localmente desaparecidas y dos extintas, *Coragyps occidentalis* y *Ectopistes migratorius*. La avifauna de Cueva Marmota se limita a pertenecientes a ocho taxa encontrados también en Cueva Sandía. Dos registros nuevos de *Gymnogyps californianus* se reportan en estos sitios, así como registros nuevos de *Lagopus* sp., *Aegolius funereus* y *Micrathene whitneyi* para Nuevo México. Dos nuevos análisis de radiocarbono del fósil *G. californianus* de las Cuevas Sandía y Marmota arrojaron una antigüedad de  $10\,795 \pm 50$  y  $25\,090 \pm 220$  <sup>14</sup>C años antes del presente, respectivamente. Estas colecciones proveen nueva evidencia de la existencia de comunidades de aves mixtas en Nuevo México durante el Pleistoceno tardío, que son similares a otras avifaunas de cuevas de edad comparable ubicadas en las regiones de la Gran Depresión y las Montañas Rocallosas. Las aves de Cueva Sandía que se encuentran en otras avifaunas fósiles incluyen especies que actualmente se encuentran en la tundra ártica y boreal, y en estepas, así como en comunidades de ambientes xerofíticos abiertos. Esta colección provee evidencia adicional de la existencia de ambientes de estepa-tundra, arbustivos y boscosos sub-alpinos a elevaciones bajas en el oeste de Norte América durante el Pleistoceno tardío.

Sandia Cave (35°15'N, 106°24'W) is a natural solution tunnel 138 m long and 2–4 m in diameter located 100 m above the base of a vertical limestone cliff in Las Huertas Canyon, New Mexico, at an elevation of 2165 m (Haynes and Agogino 1986, Thompson and Morgan 2001; Fig. 1). This area is in upper pinyon-juniper woodland (*Pinus edulis* and *Juniperus monosperma*) mixed with Gambel's oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus montanus*), and yucca (*Yucca* spp.). A few ponderosa pines (*P. ponderosa*) occur in the drainage at the base of the cliff where the cave is located. Archaeological investigations in this cave were initiated in 1936–1937 by Frank Hibben and Wesley Bliss. Hibben continued these excavations from 1938–1941 (Hibben 1937, 1941, Haynes and Agogino 1986).

There has been considerable controversy over the radiocarbon dates from Sandia Cave. Dates presented by Hibben (1955) were invalidated when it could not be shown that they were truly determined

Manuscript received 6 September 2005; accepted 17 February 2006.

<sup>1</sup> Corresponding author. E-mail: emslies@uncw.edu

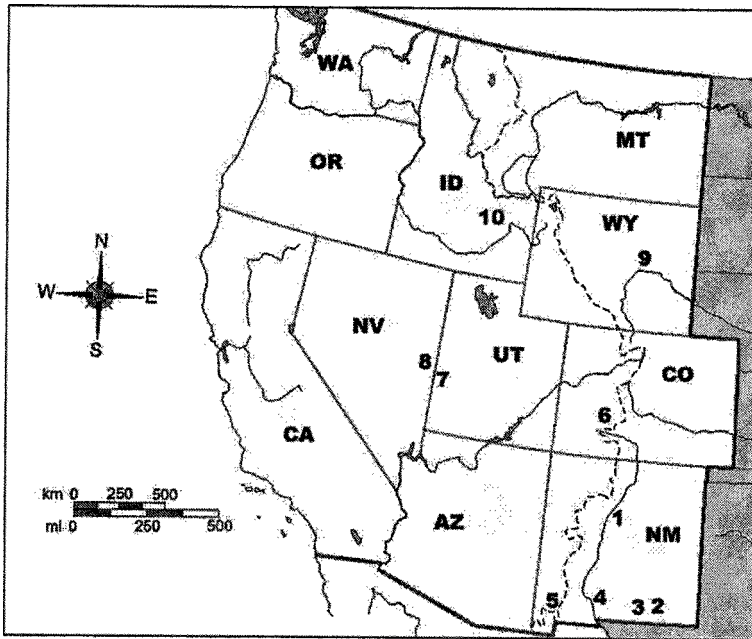


FIGURE 1. Map of the western U.S. showing the locations of sites discussed in the text: 1) Sandia and Marmot Caves, 2) Dark Canyon Cave, 3) Rocky Arroyo Cave (also known as Burnet Cave), 4) Conkling Cavern and Shelter Cave, 5) Howell's Ridge Cave, 6) Haystack Cave, 7) Crystal Ball Cave, 8) Smith Creek Cave, 9) Little Box Elder Cave, and 10) Rattlesnake Cave. Shaded areas represent lakes and estuaries. The dashed line indicates the continental divide and solid lines are rivers. State abbreviations are: WA = Washington, OR = Oregon, CA = California, ID = Idaho, NV = Nevada, AZ = Arizona, UT = Utah, MT = Montana, WY = Wyoming, CO = Colorado, and NM = New Mexico.

by radiocarbon analysis (Johnson 1957). Haynes and Agogino (1986) completed three radiocarbon dates on large mammal bones from Sandia Cave that ranged in age from 11 850–13 700  $^{14}\text{C}$  years before present (B.P.). These dates, as well as the presence of nine extinct megafauna that have been dated elsewhere as older than 10 000 B.P. (Mead and Meltzer 1984), infer a late Pleistocene age for the site and deposits. Based on this evidence, the avian fossils recovered from Sandia Cave presented here are all assumed to represent one assemblage that dates to the late Pleistocene.

We present the first descriptions and identifications of avian fossils from this important site, as well as a small collection of bird bones from nearby Marmot Cave (also known as Davis Cave; G. Morgan, New Mexico Museum of Natural History, pers. comm.) located 100 m north of Sandia Cave (Thompson and Morgan 2001). We also provide biogeographical and paleoecological interpretations of the avifaunas on both a local and regional scale, and a regional comparison of the fossil avifaunas with other late Pleistocene sites in New Mexico and the Great Basin and Rocky Mountain regions.

## METHODS

Avian remains were identified by comparison with the skeletal collection at the U.S. National Museum,

Smithsonian Institution, Washington, DC. Terminology follows that of Howard (1929). All measurements were completed with digital calipers to the nearest 0.1 mm using the techniques described by von den Driesch (1976). Minimum number of individuals of each species was calculated by counting the most common element of the same side. Taxonomy follows the American Ornithologists' Union (1998) through the forty-sixth supplement (Banks et al. 2005). Radiocarbon analysis was completed at the Center for Accelerator Mass Spectrometry (CAMS), Lawrence Livermore National Laboratory, Livermore, California. The fossil collections are housed at the Maxwell Museum of Anthropology, University of New Mexico, Albuquerque. As these fossils are part of an archaeological collection, no catalogue numbers have been assigned to the specimens.

## RESULTS

A complete list of all identified taxa, with numbers of identifiable bones and minimum number of individuals represented, is provided in Table 1. Here, we provide details for osteological identification of the taxa that are unusual, extinct, or extralimital to New Mexico and the region surrounding Sandia Cave.

A distal symphysis of a mandible was identified as *Coragyps occidentalis* (extinct vulture; Miller 1909). This specimen is distinctly larger than the symphyses

of *Cathartes aura* (Turkey Vulture) and *Coragyps atratus* (Black Vulture; Table 2) and smaller than *Gymnogyps californianus* (California Condor). It is similar to *C. atratus* and *Sarcoramphus papa* (King Vulture) in that the symphysis is relatively deeper than it is wide (Table 2; symphysis is only slightly deeper than it is wide in *C. aura*). Although the specimen is similar in size to *S. papa*, the position of foramina on the internal lateral sides of the symphysis are most similar to *Coragyps atratus*. *Coragyps occidentalis* was distinctly larger than *C. atratus* based on measurements of the skull, sternum, and pelvis (Miller 1909) as well as the coracoid and limb bones (Howard 1968). Four other bones, a medial right coracoid from Marmot Cave and a cervical vertebra, first pedal phalanx, and unguis phalanx from Sandia Cave, compare well in size and characters to the extant *Gymnogyps californianus*. Radiocarbon analysis of the coracoid from Marmot Cave and the cervical vertebra from Sandia Cave produced dates of  $10\,795 \pm 50$  (CAMS 123881) and  $25\,090 \pm 220$  (CAMS 123916)  $^{14}\text{C}$  years B.P., respectively.

The distal halves of a right femur and right tarsometatarsus compare well in size and characters, including muscle scars, to *Buteo lineatus* (Red-shouldered Hawk; Table 3). This species currently occurs in the eastern U.S. and coastal California and Baja in wooded and riparian habitats (Crocoll 1994). Recently, it has been expanding further inland in the western U.S., occurring regularly as a vagrant and with one breeding record in Arizona (Glinski 1998), but it is hypothetical in New Mexico (Hubbard 1978). The record here is considered extralimital.

A fragmentary coracoid, humerus, two carpometacarpi, and a tarsometatarsus were identified by size and characters as *Centrocercus urophasianus* (Greater Sage-Grouse). These specimens are distinctly larger than *Tympanuchus phasianellus* (Sharp-tailed Grouse), *T. cupido* (Greater Prairie-Chicken), and *Dendragapus obscurus* (Blue Grouse). A recently recognized species, *C. minimus* (Gunnison Sage-Grouse), is also smaller than *C. urophasianus* (Hupp and Braun 1991, Young et al. 2000), but no specimens were available for comparison here. Fourteen bones compare well with *Lagopus* spp. (Fig. 2), but most are too fragmentary for specific identification. Comparative measurements of the fossil carpometacarpi with *L. lagopus* (Willow Ptarmigan), *L. muta* (Rock Ptarmigan), and *L. leucura* (White-tailed Ptarmigan; Table 4) indicate that the fossils are closest to the last species in size, but are more robust.

Fossils identifiable as *Dendragapus obscurus* are the most abundant in the cave deposits. All these fossils are distinctly larger and more robust than *Tympanuchus phasianellus*, *T. cupido*, and *Falci pennis canadensis* (Spruce Grouse), and most closely match *D. obscurus* in size and characters.

*Meleagris gallopavo* (Wild Turkey) is represented by one bone at Marmot Cave and three from Sandia Cave. All specimens referred here are distinguishable from other Galliformes by their large size and compare well in size and characters to living *M. gallopavo*. The tibiotarsus from Marmot Cave is within the size range of female *M. gallopavo* (Stead-

man 1980). None of the specimens referred here appear to represent the smaller and distinct fossil species, *M. crassipes*, which has been reported from other late Pleistocene sites in New Mexico (Rea 1980, Steadman 1980).

One bone, a humeral half of a left coracoid, is tentatively referred to *Callipepla* cf. *C. squamata* (Scaled Quail). The fossil has a larger and more robust shaft than that of *Colinus virginianus* (Northern Bobwhite) and is smaller and less robust than *Oreortyx pictus*. It compares well with *Callipepla*, especially *C. squamata*, but not *C. gambelii* (Gambel's Quail). The former species and the fossil specimen have a relatively shorter shaft and smaller distance between the coraco-humeral surface and the procoracoid than the latter. Tatchl (1967) found *C. squamata* to be a permanent resident in the Sandia Mountains, especially in lower vegetative zones.

A distal half of a right ulna is tentatively referred to the extinct *Ectopistes migratorius* (Passenger Pigeon). The specimen is larger than *Zenaidura macroura* (Mourning Dove) and *Z. asiatica* (White-winged Dove), and smaller than *Patagioenas fasciata* (Band-tailed Pigeon).

A left tibiotarsus missing the distal end is tentatively referred to *Glaucidium* cf. *G. gnoma* (Northern Pygmy-Owl). The specimen measures 4.3 mm and 4.9 mm in proximal breadth and depth, respectively, and 2.2 mm and 1.9 mm in least breadth and depth of shaft. Although the fossil is similar in size to *Micrathene*, the fossil has a more robust outer cnemial crest, a more angular proximal shaft, and a relatively longer fibular crest; these features are similar to *Glaucidium gnoma*. *G. brasilianum* (Ferruginous Pygmy-Owl) is slightly larger and more robust than *G. gnoma*, and comparative measurements (Emslie 1998:table 12) indicate that the fossil is most similar to *G. gnoma* in size.

*Micrathene whitneyi* (Elf Owl) is represented by a complete left tarsometatarsus that measures 23.0 mm in length, 4.1 mm and 3.0 mm in proximal breadth and depth, respectively, 2.2 mm and 1.7 mm in least breadth and depth of shaft, and 4.8 mm in distal breadth. This specimen compares best to *Micrathene whitneyi* versus *Glaucidium gnoma* and *Aegolius* spp. (Fig. 3). A complete right and left tarsometatarsus are referable to *Aegolius funereus* (Boreal Owl). The right bone measures 24.4 mm in length, 7.7 mm and 4.6 mm in proximal breadth and depth, respectively, 4.7 mm and 2.3 mm in least breadth and depth of shaft, and 8.2 mm in distal breadth. The left measures 22.9 mm in length, 6.7 mm and 4.6 mm in proximal breadth and depth, respectively, 3.8 mm and 2.0 mm in least breadth and depth of shaft, and 7.1 mm in distal breadth. Tarsometatarsi of *A. acadicus* (Northern Saw-whet Owl) and *A. funereus* are easily distinguished by the relatively broader ends and more robust shaft in the latter species (Emslie 1985:table 5).

A complete left tibiotarsus compares well to extant *Nucifraga columbiana* (Clark's Nutcracker) in size and characters and is the first fossil record of this species from New Mexico. The tibiotarsus of this distinct species has excavations on the proximal end and distal intercotylar area, as well as size and

TABLE 1. Fossil avifauna of Sandia and Marmot Caves, New Mexico, with number of identified bones for each taxon (calculated minimum number of individuals in parentheses). Comparison of shared species identified from other late Pleistocene sites from similar geographic regions also is given. Site abbreviations are: LBE = Little Box Elder Cave, Wyoming (Emslie 1985); RC = Rattlesnake Cave, Idaho (Steadman et al 1994); CBC = Crystal Ball Cave, Utah (Emslie and Heaton 1987); SCC = Smith Creek Cave, Nevada (Howard 1952); DCC = Dark Canyon Cave, New Mexico (Howard 1971); CC = Conkling Cavern, SC = Shelter Cave, and RA = Rocky Arroyo (Burnet Cave), New Mexico (Howard and Miller 1933); HR = Howell's Ridge, New Mexico (Howard 1962). Extinct taxa are marked with †, while ‡ indicates extralimital species in the region of Sandia Cave today.

Taxon	Sandia	Marmot	LBE	RC	CBC	SCC	DCC	CC	SC	RA	HR
<b>Vulturidae</b>											
<i>Coragyps occidentalis</i> (extinct vulture)†	1 (1)					x	x	x			x
<i>Cathartes aura</i> (Turkey Vulture)	1 (1)							x	x	x	
<i>Gymnogyps californianus</i> (California Condor)‡	3 (1)	1 (1)				x	x	x	x	x	x
<b>Anatidae</b>											
<i>Lophodytes cucullatus</i> (Hooded Merganser)	6 (2)										
Anatidae sp.	2		x	x		x					
<b>Accipitridae</b>											
<i>Accipiter striatus</i> (Sharp- shinned Hawk)	1 (1)		x		x				x		
<i>Accipiter cooperii</i> (Cooper's Hawk)	2 (1)						x			x	
<i>Buteo lineatus</i> (Red- shouldered Hawk)‡	2 (1)										
<i>Buteo</i> sp.	14		x		x						x
<i>Aquila chrysaetos</i> (Golden Eagle)	2 (1)		x		x	x	x	x	x		x
Accipitridae sp.	8	1	x		x						
<b>Falconidae</b>											
<i>Falco sparverius</i> (American Kestrel)	2 (1)		x	x		x	x	x	x		
<i>Falco</i> cf. <i>F. peregrinus</i> (Peregrine Falcon)	1 (1)								x		
<i>Falco peregrinus</i> or <i>F.</i> <i>mexicanus</i> (Peregrine or Prairie Falcon)	1										
<i>Falco</i> cf. <i>F. mexicanus</i> (Prairie Falcon)‡	1 (1)		x	x	x	x	x			x	x
<b>Phasianidae</b>											
<i>Centrocercus</i> <i>urophasianus</i> (Greater Sage-Grouse)	5 (2)		x	x	x	x		x	x		x
<i>Lagopus</i> sp. (ptarmigan)‡	13 (3)		x								
<i>Dendragapus obscurus</i> (Blue Grouse)	174 (24)	1 (1)	x		x						
<i>Meleagris gallopavo</i> (Wild Turkey)	3 (1)	1 (1)					x	x	x	x	x
<i>Callipepla</i> cf. <i>C.</i> <i>squamata</i> (Scaled Quail)	1 (1)								x		
Phasianidae sp.	1		x								
Charadriiformes sp.		1									

TABLE 1. Continued.

Taxon	Sandia	Marmot	LBE	RC	CBC	SCC	DCC	CC	SC	RA	HR
Columbidae											
<i>Zenaidura macroura</i> (Mourning Dove)	1 (1)		x	x		x	x		x		
cf. <i>Ectopistes migratorius</i> (Passenger Pigeon) <sup>†*</sup>	1 (1)		x				x				
Strigidae											
<i>Bubo virginianus</i> (Great Horned Owl)	7 (1)		x		x	x	x		x	x	
cf. <i>B. virginianus</i> (juv.)	1 (1)										
<i>Glaucidium</i> cf. <i>G. gnoma</i> (Northern Pygmy-Owl)	1 (1)										
<i>Micrathene whitneyi</i> (Elf Owl) <sup>‡</sup>	1 (1)										
<i>Asio</i> cf. <i>A. otus</i> (Long- eared Owl)	2 (1)		x	x	x			x			x
<i>Asio flammeus</i> (Short- eared Owl)	1 (1)		x	x		x	x			x	
<i>Asio</i> cf. <i>A. flammeus</i>	1										
<i>Asio</i> sp.	4		x		x						
<i>Aegolius</i> cf. <i>A. acadicus</i> (Northern Saw-whet Owl)	1 (1)		x			x			x		
<i>Aegolius funereus</i> (Boreal Owl) <sup>‡</sup>	2 (1)		x						x		
cf. <i>A. funereus</i>	1										
<i>Aegolius</i> sp.	1										
Picidae											
<i>Colaptes auratus</i> (Northern Flicker)	13 (3)	1 (1)	x					x	x		
Picidae sp.	1										
Corvidae											
cf. <i>Cyanocitta stelleri</i> (Steller's Jay)	1 (1)										
<i>Nucifraga columbiana</i> (Clark's Nutcracker)	1 (1)		x			x					
<i>Pica hudsonia</i> (Black- billed Magpie)	1 (1)	1 (1)	x	x		x			x		
<i>Corvus corax</i> (Common Raven)	1 (1)		x			x	x	x	x		x
Passeriformes sp.	6	2	x	x	x	x	x				
Total	293 (65)										

TABLE 2. Comparative mean measurements (mm ± SD) of the proximal breadth and depth of the mandibular symphysis in extant *Cathartes aura* (Turkey Vulture), *Sarcoramphus papa* (King Vulture), and *Coragyps atratus* (Black Vulture) compared to the fossil of *Coragyps occidentalis* (extinct vulture) from Sandia Cave, New Mexico.

Taxon	Sex	Proximal breadth	Proximal depth
<i>Cathartes aura</i> (n = 4)	F	9.6 ± 0.2	11.0 ± 0.8
<i>C. aura</i> (n = 2)	M	8.8 ± 0.2	10.2 ± 1.0
<i>Sarcoramphus papa</i> (n = 3)	F	14.0 ± 0.3	15.7 ± 0.8
<i>S. papa</i> (n = 1)	M	14.1	14.7
<i>S. papa</i> (n = 4)	U	13.8 ± 0.6	15.2 ± 0.6
<i>Coragyps atratus</i> (n = 3)	F	9.7 ± 0.2	13.7 ± 0.3
<i>C. atratus</i> (n = 3)	M	9.6 ± 0.4	13.4 ± 0.3
<i>C. occidentalis</i>	U	~10.8	15.5

TABLE 3. Mean comparative measurements (mm  $\pm$  SD) of *Buteo lineatus* (Red-shouldered Hawk) leg elements. Measurements are distal breadth and depth of femora (FDB and FDD) and distal breadth (TDB) and middle trochlea breadth and depth (TMTB and TMTD) of tarsometatarsi compared to two specimens referred to this species from Sandia Cave, New Mexico.

Taxon	Sex	FDB	FDD	TDB	TMTB	TMTD
<i>Buteo lineatus</i> (n = 5)	F	13.7 $\pm$ 0.5	10.9 $\pm$ 0.5	12.3 $\pm$ 0.7	3.8 $\pm$ 0.6	4.8 $\pm$ 0.3
<i>B. lineatus</i> (n = 5)	M	13.2 $\pm$ 0.6	10.2 $\pm$ 0.6	12.0 $\pm$ 0.5	3.5 $\pm$ 0.2	4.4 $\pm$ 0.4
Sandia Cave specimens		14.4	11.1	11.4	3.5	4.9

position of the fibular crest, that are similar to those in the fossil. The fossil has a slightly longer cnemial crest than *Gymnorhynchus cyanocephalus* (Pinyon Jay). It is distinctly smaller than *Cyanocitta stelleri* (Steller's Jay), and larger than male *Perisoreus canadensis* (Gray Jay). Male and female *Aphelocoma coerulescens* are relatively more robust.

## DISCUSSION

The avifauna of Sandia Cave is comprised of at least 30 taxa, including two extinct and seven extralimital species, while that of Marmot Cave is limited to eight taxa with all but one (Charadriiformes sp.) shared with Sandia Cave. One shared taxon, *Gymnogyps californianus* (California Condor), is extralimital to New Mexico today, and its identification here provides two new fossil localities for this species in the western U.S. It has been absent from the inland west, and limited to coastal regions from Mexico to Oregon, since the end of the Pleistocene (Emslie 1987). The two new radiocarbon dates for this species reported here support this conclusion. The large, extinct vulture, *Coragyps occidentalis*, has been recorded from at least 13 other sites from Florida to California, including three sites in New Mexico (Howard 1968). *C. occidentalis* and *G. californianus* were specialized feeders at carcasses of large mammals (Hertel 1992, 1994) and both disappeared from

the inland west, with *C. occidentalis* also becoming extinct, at the same time as the late Pleistocene megafauna  $\sim$ 10 000 B.P.

*Lagopus* sp. (ptarmigan) is also an extralimital taxon at Sandia Cave. Although the size and characters of the fossils are similar to those of living *L. lagopus* and *L. muta*, we cannot reject the possibility that the fossils represent a large, temporal form of *L. leucura*. The latter species commonly occurs in alpine tundra throughout the southern Rocky Mountains and south to New Mexico today (Braun et al. 1993), so its presence in the fossil record here is more likely than that of the other two *Lagopus* species.

Seven species of owls were identified from Sandia Cave, of which three are rare or extralimital in this region of New Mexico. The specimens of *Micrathene whitneyi* and *Glauucidium gnoma* are the first fossil records of these species from New Mexico. The former is fairly common in the southwestern part of the state today (de la Torre 1990, Henry and Gehlbach 1999), while the latter is found in areas dominated by yellow or ponderosa pines at elevations above  $\sim$ 1800 m (Ligon 1961, Holt and Petersen 2000). *Aegolius funereus* has been reported from only one other late Pleistocene site in New Mexico and one archaeological site (Emslie 1981). Modern records of this species in New Mexico (Stahlecker and Rawinski 1990) and Colorado (Baldwin and Koplin 1966) have led to suggestions that these are relict local breeding populations of a more widespread Pleistocene population (Stahlecker and Duncan 1996).

Fossil records of *Ectopistes migratorius* are sporadic in western North America. Two records from California (Howard 1937) and one from New Mexico (Howard 1971) were dated to the late Pleistocene. Additional archaeological records from New Mexico (Hargrave and Emslie 1980) and Utah (Parmalee 1980) provide supporting evidence for a widespread western distribution of *E. migratorius* during the Holocene.

## BIOGEOGRAPHICAL COMPARISONS AND PALEOECOLOGY

The avifauna of Sandia Cave represents environmental conditions ranging from desert and desert grassland (*Falco mexicanus*, *Micrathene whitneyi*, *Callipepla squamata*) to subalpine forest (*Dendragapus obscurus*, *Aegolius funereus*, *Nucifraga columbiana*) and alpine tundra (*Lagopus* sp.), a strong indication of a disharmonious (Lundelius 1989), or

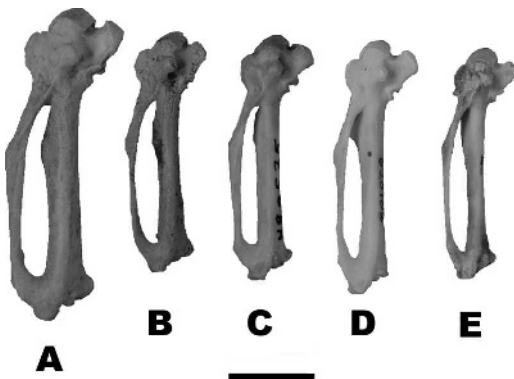


FIGURE 2. Internal view of left carpometacarpi of fossil *Dendragapus obscurus* (a) and *Lagopus* sp. (b) from Sandia Cave, New Mexico, compared with a recent female *L. lagopus* (c), male *L. muta* (d), and unsexed *L. leucura* (e). Scale bar = 1 cm.

TABLE 4. Mean comparative measurements (mm  $\pm$  SD) of extant *Lagopus lagopus* (Willow Ptarmigan), *L. muta* (Rock Ptarmigan), and *L. leucura* (White-tailed Ptarmigan) carpometacarpi with three specimens of *Lagopus* sp. from Sandia Cave, New Mexico.

	Sex	Length	Proximal depth	Least breadth shaft	Distal depth
Recent					
<i>L. lagopus</i> (n = 12)	M	33.5 $\pm$ 1.4	9.5 $\pm$ 0.3	3.4 $\pm$ 0.2	6.7 $\pm$ 0.7
<i>L. lagopus</i> (n = 8)	F	31.6 $\pm$ 1.3	8.9 $\pm$ 0.4	3.5 $\pm$ 0.2	6.5 $\pm$ 0.3
<i>L. muta</i> (n = 7)	M	32.8 $\pm$ 0.3	9.5 $\pm$ 0.4	3.2 $\pm$ 0.2	6.5 $\pm$ 0.4
<i>L. muta</i> (n = 7)	F	31.8 $\pm$ 1.3	9.2 $\pm$ 0.3	3.1 $\pm$ 0.3	6.4 $\pm$ 0.7
<i>L. leucura</i> (n = 6)	2M, 3F, 1U	29.1 $\pm$ 0.5	7.9 $\pm$ 0.2	2.7 $\pm$ 0.3	5.4 $\pm$ 0.3
Sandia Cave (n = 3)		29.9 $\pm$ 0.1	8.7 $\pm$ 0.0	3.2 $\pm$ 0.4	5.8 $\pm$ 0.1

nonanalog (Stafford et al. 1999), community structure (species that were sympatric in the past, but are allopatric today) during the late Pleistocene. The fossil mammals from Sandia Cave also represent a broad ecological range, including species associated with open grassland environments and montane and subalpine regions (Thompson and Morgan 2001), similar to many other late Pleistocene vertebrate localities in North America (Webb et al. 2003).

Evidence for nonanalog plant and animal communities in western North America during the late Pleistocene is well documented (Lundelius et al. 1983, Spaulding et al. 1983, Webb et al. 2003). Stafford et al. (1999) used accelerator mass spectrometry  $^{14}\text{C}$  dates obtained from 60 bones from two North

American and one Russian site to demonstrate that numerous mammalian taxa that are allopatric today occurred sympatrically between 12 000 and 22 000 B.P. Webb et al. (2003) also found that vertebrate communities from the late Pleistocene frequently contained living species that no longer overlap geographically, for example arctic and boreal voles with grassland taxa. These communities of both mammals and birds represent assemblages and environments that no longer exist today.

The fossils from Sandia and Marmot Caves can be compared to five other late Pleistocene collections from New Mexico, three from the Great Basin, and one from the Great Plains (Fig. 1, Table 1); Emslie (1985) and Emslie and Heaton (1987) previously reviewed and compared several other smaller fossil avifaunas from this region. In particular, Sandia Cave shares numerous taxa, including vultures, raptors (eagles, hawks, falcons, and owls), turkey, and grouse, with all these other sites. The most comparable site to Sandia Cave within New Mexico is Shelter Cave in Dona Ana County (Howard and Miller 1933). This extensive collection also reflects a nonanalog community structure, with taxa representative of Upper Sonoran and desert grassland (*Callipepla squamata*, *Geococcyx* spp., *Calamospiza melanocorys* [Lark Bunting]) to subalpine forest environments (*Aegolius funereus*, *A. acadicus*).

The avifauna of Sandia Cave is also similar to that of caves in the Great Basin and Rocky Mountain region including Crystal Ball Cave, Utah, dated at 12 980 to 23 000+ B.P. (Emslie and Heaton 1987), Rattlesnake Cave, Idaho, dated post-11 000 B.P. (Steadman et al. 1994), Smith Creek Cave, Nevada (Howard 1952), and Little Box Elder Cave, Wyoming (Emslie 1985). The collection from Crystal Ball Cave contains an assortment of late Pleistocene species. Over 400 bird bones were recovered from this site (Emslie and Heaton 1987) and, similar to Sandia Cave, *Dendragapus obscurus* was the most abundant taxon. Moreover, *D. obscurus* is common from other Pleistocene deposits in Wyoming, California, Idaho, and Oregon (Emslie and Heaton 1987). *Centrocercus urophasianus* was also well represented at Crystal Ball Cave. Steadman et al. (1994) suggested that the abundance of grouse bones in late Pleistocene records may be due to selective predation by large birds of prey. The frequent occurrence of predatory birds in



FIGURE 3. Anterior view of left tarsometatarsi of (a) recent *Glaucidium gnoma* male (USNM 621145), (b) recent unsexed *Micrathene whitneyi* (USNM 502286), and (c) fossil *M. whitneyi* from Sandia Cave, New Mexico. Scale bar = 1 cm.

these fossil avifaunas lends support to this conclusion.

Although primarily mammal remains were reported from Haystack Cave, Colorado, the geology of this site is very similar to that of Sandia Cave (Emslie 1986, 2002). Haystack Cave is a lava tube at an elevation of 2438 m. A recent excavation of Haystack Cave reported radiocarbon dates on mammal bones ranging from 19 990 to 12 910 B.P. (Emslie 2002). The identification of five species of *Sorex* led Emslie (2002) to hypothesize the presence of both a mixed sagebrush steppe and subalpine forest environment in this region during the late Pleistocene. The type of mixed plant community structure present at Haystack Cave is similar to that of the hypothesized habitat surrounding Sandia Cave during the late Pleistocene.

The comparisons presented here indicate broad similarities in avian communities throughout the Great Basin and Rocky Mountain regions during the late Pleistocene. These communities were dominated by species of open steppe-tundra, shrub, and forested habitats that occurred south of the ice sheets at that time. Climatic conditions after the last glacial maximum at ~18 000 B.P. were characterized by cool, wet summers and mild winters (Spaulding et al. 1983, Pielou 1991) which facilitated the development of the nonanalog communities that became widespread at that time. The fossils from Sandia and Marmot Caves add two more late Pleistocene avifaunas to the record for the western U.S. The unusual records of birds reported from these sites make these collections valuable to continuing studies of late Pleistocene paleoecology and avian community structure.

We thank Gary Morgan for bringing this collection to our attention and for providing information on plant communities at Sandia Cave. Bruce Huckell, Maxwell Museum of Anthropology, University of New Mexico, processed the loan of the Sandia Cave fossils. We also thank Storrs Olson, Helen James, and James Dean for their help with the skeletal collection at the Smithsonian Institution, and Janet Hinshaw (University of Michigan Museum of Zoology, Ann Arbor), Andy Johnson (Museum of Southwestern Biology, Albuquerque, New Mexico), Stephen Rogers and Andrew Rogers (Carnegie Museum of Natural History, Pittsburgh), and Tom Webber (Florida Museum of Natural History, Gainesville) for assistance with skeletal measurements of ptarmigans. L. Sayigh and A. Pabst loaned the digital camera equipment used for photographing specimens. We are very grateful to Kena Fox-Dobbs for coordinating the radiocarbon analyses, including collagen extraction at the University of California Santa Cruz Stable Isotope Laboratory and analysis at the Center for Accelerator Mass Spectrometry, (CAMS), Lawrence Livermore National Laboratory. We also thank members of RLB's Honors committee, Mike McCartney, David Webster, and Mark Galizio, for providing support, motivation, and useful suggestions throughout this project. Carlos Zavalaga provided the Spanish abstract. Amadeo

Rea and Jim Mead reviewed an earlier version of the manuscript and provided many useful comments.

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