

CONKLING'S ROADRUNNER—A SUBSPECIES OF
THE CALIFORNIA ROADRUNNER?

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Abstract.—A fossil roadrunner from interstadial deposits (ca. 33,590 BP) in New Mexico is identified as *Geococcyx californianus*. Fossil remains from California, dating from the subsequent late Wisconsinan stadial, have been assigned to the same taxon. However, approximately contemporaneous populations of larger-sized individuals occurring inland have been named *G. conklingi*. This taxon also has been recognized as surviving into the early Holocene before becoming extinct. This geographic and temporal pattern is hypothesized as being the result of local adaptations for temperature regulation: hot summer temperatures result in heat stress, resulting in selection against large individuals that otherwise would be best adapted for winter cold; absence of hot temperatures allows selection for large-sized individuals. The inland population of large-sized roadrunners, then, was a geographic and temporal subspecies, *G. californianus conklingi*.

Conkling's Roadrunner (*Geococcyx conklingi*) was described by Howard (1931) from late Pleistocene deposits of Conkling Cavern, Dona Ana Co., New Mexico (Fig. 1). The species was characterized by size greater than that of the living roadrunner, *Geococcyx californianus*. Specimens from a nearby site (Shelter Cave) also were referred to this species (*G. californianus* also was reported, but some specimens definitely were modern and the remainder probably so).

Since that time, *G. conklingi* has been reported from the late Pleistocene sites of San Josecito Cave, in southern Nuevo Leon, Mexico (L. Miller, 1943); and Dark Canyon Cave (Howard, 1971), southwest of Carlsbad, Eddy Co., New Mexico. Gehlbach and Holman (1974) reported its presence in Holocene deposits (<6,000 BP) of Pratt Cave in the Guadalupe Mountains of Culberson Co., Texas; Rea (1980) confirmed the identification, "though it is slightly larger and somewhat different in characters from the type."

Fossil *G. californianus* have been reported only from the late Pleistocene asphalt deposits of California: Rancho La Brea, Los Angeles Co.; Carpinteria, Santa Barbara Co.; and McKittrick, Kern Co. (Larson, 1930). Thus the literature indicates the presence of *G. californianus* in California at the same time as *G. conklingi* occurred inland, with the latter persisting well into the Holocene. In this paper, we add two pertinent records of fossil roadrunners and attempt to clarify the taxonomy and paleoecology of the two taxa.

MATERIALS AND RESULTS.—One specimen comes from the Khulo Site (University of Texas at El Paso—UTEP—Loc. 21), Dona Ana Co., New Mexico, some 80 km west of the type locality of *G. conklingi*. This specimen, a cranium (UTEP 21-69), is referred tentatively to *G. conklingi*. Three cranial measurements are given for a sample of modern roadrunners by Larson (1930). Of these, length of cranium may be taken directly on 21-69, but Larson's diagram is too vague to be sure the measurements are strictly comparable. Larson's largest length measurement ($n = 16$) is 37.8 mm, compared to a measurement of 38.2 mm on 21-69. Despite the loss of one postorbital process, the width of the skull through the postorbital processes may be closely estimated on

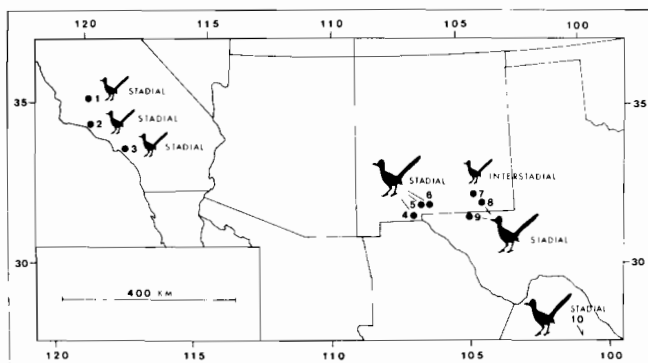


FIG. 1.—Fossil roadrunner sites. Size of roadrunner figures indicates the taxon from the site (large, *Geococcyx californianus conklingi*; small, *G. c. californianus*). 1, McKittrick; 2, Carpinteria; 3, Rancho La Brea; 4, Khulo Site (Holocene); 5, Shelter Cave; 6, Conkling Cavern; 7, Dry Cave; 8, Dark Canyon Cave; 9, Pratt Cave (Holocene); and 10, San Jasecito Cave (off diagram).

21-69 as 29.8 mm (27.1 mm plus an estimated missing 2.7 mm). This compares to a maximum width of 29.4 mm on Larson's (1930) modern material ($n = 15$). The Khulo specimen, then, certainly represents a very large roadrunner, quite possibly *G. conklingi*.

The Khulo specimen almost certainly is Holocene in age. The site is a lava pit forming a natural trap and also serving as a roost for birds of prey (Smartt, 1977). Testing of the sediments in 1970 revealed a fauna mostly typical of the area today, although presence of the meadow vole (*Microtus pennsylvanicus*) was reported by Smartt (1977) and the Mexican wood rat (*Neotoma mexicana*) has been identified recently (Harris, in prep.). A series of radiocarbon dates on wood and charcoal (*Microtus* level, $1,700 \pm 70$ BP, TX-1557; levels immediately under *Microtus* level, $1,550 \pm 60$ and $8,210 \pm 220$ BP, TX-1556A and B, respectively) indicated that mixing has occurred in the loose fill. Pleistocene fill either is absent or occurs only at depths greater than those sampled. The cranium was recovered from the surface away from the test pit.

Another specimen (Fig. 2), a humerus (UTEP 26-152), comes from interstadial deposits of Dry Cave, Eddy Co., New Mexico, about 23 km west of Carlsbad and ca. 200 km east of Conkling Cavern. A radiocarbon date on bone carbonates is $33,590 \pm 1500$ (TX-1773) BP. The associated fauna indicates climatic conditions warmer and drier than during the subsequent Wisconsinan maximum, but still with greater effective moisture than at present (Harris, 1977). The humerus seems clearly referable to *G. californianus* in measurements (Table 1) and in the character of the ectepicondylar prominence. The latter was described by Howard (1931) as forming a more acute angle with the shaft in *G. conklingi* than in *G. californianus*, such that a line drawn at a 90° angle to the proximal surface of the prominence reaches "no farther than the external condyle in *conklingi*, while in *californianus* it reaches beyond the internal condyle, . . ." In the Dry Cave specimen, such a line runs medial to the internal condyle. Thus *G. californianus* was present in the Pleistocene far east of the previously known Pleistocene occurrences of *G. californianus*, east of the type locality of Conkling's Roadrunner, and in the same area as the stadial occurrence of *G. conklingi* at nearby Dark Canyon Cave.

Two specimens of *Geococcyx californianus* are known from a cave site near Jimenez, in southern Chihuahua, Mexico (UTEP Loc. 91). Although Pleistocene forms occur at the site, the cave fill is badly disturbed and the specimens could be interstadial, stadial, or Holocene (Messing, pers. comm.).

DISCUSSION.—The sketchy fossil record thus indicates that *G. californianus* occurred in the Southwest during the interstadial time represented at Dry Cave. *G. conklingi* occurred in the interior but not along the West Coast during the late Wisconsinan full-glacial and into the early Holocene, and then became extinct. Such a sequence suggests to us that *G. conklingi*

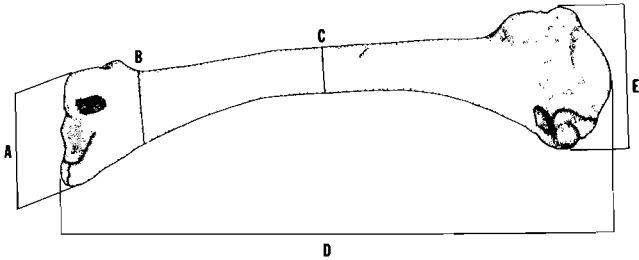


FIG. 2.—Fossil humerus (UTEP 26-152) from interstadial deposits of Dry Cave indicating where measurements were made. A, distal breadth; B, breadth above epicondyle; C, breadth of shaft; D, total length; E, greatest head breadth.

is not a separate species, but a temporal and geographic subspecies of *G. californianus*. Our reasoning follows.

Numerous late Pleistocene warm-blooded vertebrates were larger during the late Wisconsinan pluvial than the same species or their linear descendants today. In some cases, this is true only when populations from the same geographic area are compared. For example, Southwestern Common Ravens (*Corvus corax*) (Magish and Harris, 1976) and some populations of big brown bats (*Eptesicus fuscus*) (Guilday, 1967) show this pattern. In other cases, such as in Pleistocene forms of the California Condor (*Gymnogyps californianus*) and Golden Eagle (*Aquila chrysaetos*) (Howard, 1947), and cave myotis (*Myotis velifer*) (Dorsey, 1977), Pleistocene forms average larger than those in any population known today.

Although competition with other predators (McNab, 1971) or reduction in prey size (Howard, 1947) have been suggested as causes in some cases, most workers seem to prefer some aspect of climatic change. Generally, the latter arguments are based on the interaction of body size and temperature

TABLE 1.—Comparison of *Geococcyx humeri* measurements (mm).

Measurement	<i>Geococcyx conklingi</i>		<i>Geococcyx californianus</i>		
	Syntype Conkling Cavern LACM 118	Paratype Shelter Cave LACM 117	Dry Cave UTEP 26-152	Modern (Larson, 1930) range (x)	Modern UTEP range (x)
Distal breadth	11.2	11.7	10.0	8.9-10.6 (9.6) N = 20	8.8-10.2 (9.5) N = 6
Distal depth	5.8	6.5	~5.6	5.2-6.9 (5.7) N = 20	5.1-5.7 (5.3) N = 6
Breadth above epicondyle	7.1	7.3	6.1	N = 6	4.8-5.6 (5.2)
Depth above epicondyle	3.7	4.2	3.2		3.0-3.5 (3.2) N = 6
Breadth of shaft	4.3	4.5	4.3	3.0-3.8 (3.3) N = 20	3.2-3.8 (3.4) N = 6
Total length			46.4		41.6-48.3 (44.7) N = 5
Greatest head breadth			~11.7	10.4-13.6 (11.2) N = 21	10.2-11.4 (10.8) N = 7

(Bergmann's Rule, where larger body size is associated with colder temperature). The rationale behind Bergmann's Rule is that larger body size conserves heat since there is less surface area for heat loss relative to body volume. We suspect such an interaction has been operative with *Geococcyx*, but an understanding of the pattern seen in roadrunners requires consideration of Pleistocene climatic conditions.

Greater size is not a direct result of cold winters alone, or present-day populations would differ in size geographically according to winter temperatures. This does not seem to be the case, although we are unsure that such potential variation has been sufficiently studied in *Geococcyx*.

There also is evidence that late Pleistocene winter minimal temperatures (which presumably were more important than average winter temperatures) actually were less severe than at present. Both *Geococcyx conklingi* and the desert tortoise (*Gopherus agassizi*) occurred at Shelter Cave (Van Devender et al., 1976), with dates on scutes of the tortoise ranging from 11,130 to 12,520 BP (Thompson et al., 1980). The desert tortoise currently appears to be excluded from east of Cochise Co., Arizona, by low winter temperatures (Van Devender et al., 1976). Its occurrence at Shelter Cave strongly suggests that winter minima were similar to those in the upper Sonoran and Mojave deserts of today, rather than those now common in southern New Mexico. *Gopherus agassizi* also was present in the Dry Cave interstadial fauna, again suggesting moderate winter minima.

Although the late Wisconsinan stadials and interstadials probably lacked the temperature extremes of today, average cold-season temperatures probably were lower than those of today. The lack of size variability of modern roadrunner populations correlated to differences in either extreme or average winter temperatures suggests that an additional factor is involved.

During the Wisconsinan full-glacial, summer temperatures, as well as those of winter, are widely considered to have been cooler overall and to have lacked the extremes of today (Harris, 1977). The difficulty in assigning cooler summers a causative role in body size increase is the fact that even pluvial summer temperatures would not be expected to require heat conservation.

However, one characteristic of summer may be vital in temperature-size relationships. *A priori*, summer high temperatures are as likely to result in temperature regulation stress as are winter low temperatures, particularly for diurnal predators such as roadrunners. Even short periods of high temperatures would stress larger-bodied roadrunners more than smaller individuals. Thus even if larger size is of value for heat retention during the cold season, heat stress during a hot summer would counter any advantage.

Our hypothesis is that such a mechanism is at work among modern roadrunners, preventing selection for larger size among living populations in areas of cold winters. Under this hypothesis, Pleistocene populations not subjected to cold stress would be size-limited by heat stress and have body sizes about the same as in modern roadrunners, as would Pleistocene populations subjected to both cold and heat stress (as suggested for most populations of modern roadrunners). In populations stressed by the

generally cold Pleistocene winters, but not subjected to hot summer temperatures, selection for larger individuals would have occurred.

Thus the equable climate of Pleistocene California (Warter, 1976), with relatively warm winters, would favor roadrunners similar in size to those of today. Inland, away from moderating maritime influences and at generally much higher elevations, cold winter temperatures and the absence of high summer temperatures would allow selection for larger body size.

The model has implications for both interstadial and early Holocene climates. Occurrence of modern-sized roadrunners in an interstadial fauna implies at least sporadic high summer temperatures. Occurrence of large roadrunners in the early Holocene implies that non-extreme summer temperatures continued beyond the end of the Pleistocene. Van Devender (1977) has demonstrated that woodlands occupied areas of southern New Mexico and Trans-Pecos Texas that now are grassland or desert until about 8,000 BP. Appearance of the extreme summer temperatures of today may have coincided with the climatic change that finally eradicated woodlands from the lowlands of the interior Southwest.

It is not possible to say if *G. conklingi* from Pratt Cave and the large specimen from the Khulo Site date from the early Holocene cool period. The account of Pratt Cave by Gehlback and Holman (1974) states that several lines of evidence "suggest the cave deposits are more recent than 6,000 BP." Lundelius (1979) gives four radiocarbon dates, all less than 3,000 BP. Three extralimital mammals are present, as is *Equus*. The latter is believed by Lundelius to probably represent a feral domestic horse or ass, although it may be a Pleistocene form. The Khulo specimen lacks a date, but some site sediments appear to date from the early Holocene.

We may note here a potential criticism: if summer temperature stress is important, populations in low, hot deserts should be subjected to selective pressure for smaller body size. We know of no evidence that this is the case. This may indicate a lack of validity for our hypothesis, but we believe it to be more likely that decrease to less than modern body size is non-selective for other reasons (e.g., efficient utilization of prey items may require a certain minimum size).

The hypothesis is potentially falsifiable by advances in our knowledge of paleoclimatology, by the discovery of new fossil specimens, or by neontological studies indicating that either heat stress or cold stress is unimportant in *Geococcyx*.

CONCLUSIONS.—*Geococcyx conklingi* should be recognized as a temporal and geographic subspecies, *G. californianus conklingi*, rather than as a species.

Modern, late Pleistocene, and early Holocene size differences within *G. californianus* may be responses to temperature regimes: mild winters and hot summers result in modern-sized roadrunners (*G. californianus californianus*); hot summers and cold winters result in modern-sized roadrunners (*G. californianus californianus*); mild summers and cold winters result in populations with large-sized individuals (*G. californianus conklingi*).

Wisconsinan interstadial conditions in southeastern New Mexico may have included hot summer temperatures and cold average winter temperatures, without the extreme minima of today; the late Wisconsinan full-glacial of southern New Mexico probably was characterized by cold average winter temperatures and cool summers without the high maxima of today; the early Holocene (to ca. 8,000 BP or perhaps later) of southern New Mexico and Trans-Pecos Texas may have lacked the summer extremes of the present. The temperature regime of the southern Californian Pleistocene was relatively equable.

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