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8. Cine and still photographs were taken from a blind with no apparent disturbance to the animals. At other than observation times, animals were captured at the nest site and marked with paint so that we could trace their movements.
9. While the most intense emergence bouts occurred in late morning in bright sun, emergence also occurred during overcast days and from nest holes in the shade (Fig. 2). Thus, reaching a critical body temperature is not a satisfactory explanation, as animals emerged at substrate temperatures that varied from 27.5°C to more than 40°C. Temperatures at nest hole depth (50 cm) remained virtually constant during any one observation session; across days they ranged between 29° and 33°C. On 2 May 1975, we observed iguanas leaving in the rain. An animal was seen at the opening of a hole at 1000 hours. Its head was out momentarily and then gone for 2 minutes. The iguana popped up and down eight times in 42 minutes and had its head out almost 32 minutes. Within a minute, two new iguana heads appeared at the hole. After a total elapsed time of 65 minutes 40 seconds, one iguana ran off and was followed 80 seconds later by another.
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11. An impressive emergence bout was seen on 6 May 1975 (Figs. 2 and 3). At 0915 one lizard head was visible at hole 8. After 40 minutes a head appeared at hole 9 and 2 minutes later, another head at hole 7. During a 7-minute period beginning at 1013, six animals moved off to the right and then three to the left. One iguana from hole 7 went to an iguana head at hole 8 and both then left the clearing. Seven minutes later, four iguanas emerged and went to the left and were followed 6 minutes later by five more. During the next 52 minutes, no animals left the hatch area, but two departed from holes 7 and 9 oriented to the right, and another was at the entrance to 7. At this point, an iguana that had earlier gone to the right emerged from the vegetation and approached the group. After it and the others had engaged in some mutual head bobbings and tongue lickings, it moved through the group to the left. The three iguanas turned within about 5 seconds and followed the "stranger" to the left (filmed sequence). Five minutes later, five animals moved to the left and were followed 6 minutes later by first three and then five more. Three minutes later, 11 more left in over a 6-minute period in groups of two to four. Another 20 minutes of no activity was followed by a 5-minute explosive period in which 12 more emerged. From 1220 to 1225, four more animals left in groups of two. In the remaining period until 1245 hours, no more animals left the hole. A total of at least 61 lizards departed, all but nine leaving to the left. The emergence of the lizards over the 216-minute period (0910 to 1245) was not random [$\chi^2 = 85.95$ (the observation period was divided into 12 periods of equal length), d.f. = 11, $P < .001$].
12. Unlike observing at the nest site, observing at the reedy area did not require a blind. Standing or sitting quietly on shore or out in the water for several minutes was sufficient to habituate the iguanas to our presence. A portable blind was used during some photographic sessions.
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16. Quantitative results and expanded details of our studies on neonate green iguanas will be published elsewhere. Supported in part by grants from the National Institute of Mental Health, the National Science Foundation, and the Smithsonian Tropical Research Institute. We thank K. Milton and B. A. Dugan for comments on earlier drafts of this report. B. A. Dugan and J. A. Carter aided in the observations in 1976.

* Currently a visiting professor at Rockefeller University, 1230 York Avenue, New York 10021.

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Pleistocene Avifaunas and the Overkill Hypothesis

Abstract. *At the end of the North American Pleistocene, birds and mammals suffered comparable degrees of generic extinction. Both the magnitude and pattern of avian extinction are incompatible with the hypothesis that humans played a major role in causing the demise of numerous North American mammalian genera at this time.*

The hypothesis that humans played a major role in causing massive extinctions of North American mammalian genera at the end of the Pleistocene has most recently been developed by Martin (*1–5*) in a lengthy series of ingenious and influential articles. After reviewing the archeological, biological, and geological records for the North American Pleistocene, Martin concluded that "prehistoric hunters ten to fifteen thousand years ago . . . exterminated far more large animals than has modern man" (*6*), that "man and man alone was responsible for the unique wave of late Pleistocene extinctions in North America" (*7*). Martin (*2*) has appropriately labeled this hypothesized phenomenon "Pleistocene overkill."

The overkill hypothesis is readily testable. Because it states that the end of the North American Pleistocene was marked by extraordinarily high rates of extinction of mammalian genera, this hypothesis requires terminal Pleistocene mammalian generic extinctions to have been relatively greater than generic extinctions within other classes of vertebrates at this time (*8*). Since 67 genera of North American mammals are known to have become extinct during the Pleistocene, of which as many as 32 disappeared between about 13,000 and 10,000 B.P. (before the present) (*4, 5, 9*), the overkill hypothesis predicts that in nonmammalian vertebrate classes, significantly fewer than 48 percent of the genera which became extinct during the Pleistocene became extinct at the end of this epoch. This prediction may be tested against the Pleistocene record for birds (*10*).

During the North American Pleistocene, 22 genera of birds are known to have become extinct (Table 1). In order to determine the proportion of these genera which became extinct at the end of the Pleistocene, it is necessary to turn to paleontological sites which contain avifaunas demonstrably deposited between about 13,000 and 10,000 B.P.

Such sites are exceedingly rare; of them, only Rancho La Brea contains a sizable and well-analyzed fauna. Located within metropolitan Los Angeles, Rancho La Brea deposits have provided over 85,000 bones and bone fragments pertaining to over 150 species of birds (*11*). A large proportion of these avian remains came from 13 excavation units. The faunas of five of these units (pits 10, 28, 36, 37, and A) lack the large Pleistocene mammals typical of the other Rancho La Brea units, are characterized by the predominance of the modern turkey vulture (*Cathartes aura*) over the extinct western black vulture (*Coragyps occidentalis*), and show relatively low proportions of large raptors and extinct avian species. Consideration of such attributes led Howard (*11*) to conclude that, of the 13 units with sizable avifaunas, pits 10, 28, 36, 37, and A lie closest to the Pleistocene-Holocene boundary.

Only one radiocarbon date is available for these five excavation units. This date (9000 ± 80 years, UCLA-1292 BB) was obtained for human bones from pit 10 which have long been recognized as occupying a vent which "passed through older asphalt deposits containing remnants of extinct late Pleistocene animals" (*12*). As a result, this date does not apply to the extinct avian genera of this unit. However, dates ranging from approximately 13,000 to over 40,000 years ago are available for seven of the eight remaining units (*13*). Coupled with Howard's arguments, these dates strongly suggest that pits 10, 28, 36, 37, and A postdate 13,000 to 14,000 years B.P.

The birds of these five units are represented by 1658 individuals belonging to 75 genera, of which 11 are extinct in at least North America (Table 2). With the exception of the passenger pigeon (*Ectopistes migratorius*), these genera are unknown in North American faunas which unquestionably postdate 10,000 years ago. It is reasonable to conclude that these genera became extinct during very late Pleistocene times.

Other North American faunas which date, or may date, to between 13,000 and 10,000 years ago simply provide additional instances of genera documented for this time span at Rancho La Brea (*14*). These other sites combined do not provide as substantial a record of terminal

Table 1. Extinct North American Pleistocene avian genera (*22*).

Family	Genus	Modern relatives
Ciconiidae	*Ciconia*	Storks
Anatidae	*Anabernicula*	Geese, ducks
	Brantadorna	
Cathartidae	*Breagyps*	American vultures
	Teratornis	
	Cathartornis	
Accipitridae	*Spizaetus*	Buzzards, eagles
	Morphnus	
	Wetmoregyps	
	Neophrontops	
	Neogyps	
Phasianidae	*Neortyx*	Quails
Meleagrididae	*Parapavo*	Turkeys
Rallidae	*Creccoides*	Rails
Cariamidae	*Titanis*	Seriemas
Scolopacidae	*Dorypaltus*	Plovers, lapwings
Burhinidae	*Burhinus*	Thick-knees
Corvidae	*Protocitta*	Crows, jays
	Henocitta	
Icteridae	*Pandanaris*	Blackbirds, orioles
	Cremaster	
	Pyeloramphus	

Pleistocene avian extinction as does Rancho La Brea. My argument, therefore, hinges largely on the correctness of the dates for the extinct avifaunas of the five most recent Rancho La Brea excavation units.

These dates indicate that the end of the North American Pleistocene saw the extinction of at least ten genera of birds. That is, of the 22 genera of North American birds known to have become extinct during the Pleistocene, 45 percent became extinct at the end of this epoch. This figure is nearly identical to that derived for mammals, and does not support the overkill hypothesis.

The overkill hypothesis does accommodate extinctions of animals which were exterminated directly as the result of human predation, or which were dependent upon mammals which became extinct. Before it may be concluded that the avian evidence fails to support the overkill hypothesis, it is necessary to establish that these factors were not likely to have played a role in the extinction of the birds in question.

Ecological dependence upon large mammals is hard to accept for almost all of these birds (*15*). For instance, the modern relatives of the asphalt stork (*Ciconia maltha*) have in common a diet consisting largely of small vertebrates and invertebrates (*16*). Similarly, the living relatives of the tadornine Brea pigmy goose (*Anabernicula gracilenta*) (*17*) feed on plants and small vertebrates sought in the water, along muddy or sandy shores, or by grazing on dry land (*18*). Of the raptors, three (*Wetmoregyps daggetti, Morphnus woodwardi*, and *Spizaetus grinnelli*) most likely relied primarily upon small vertebrates for food, as do the extant congeneric relatives of two of them (*19*). With one exception, it is difficult to see an obligate dependence upon large mammals for the late Pleistocene vultures which became extinct, given the variable diets of their modern relatives (*20*). The one exception, Merriam's teratorn (*Teratornis merriami*), with a wing span of some 3.5 m, is related to the modern California condor (*Gymnogyps californianus*); given the size of this Pleistocene vulture and the adaptations of California condors, it is possible that these birds were dependent upon mammals which became extinct at the end of the Pleistocene. Such dependence would not have been shared by the California turkey (*Parapavo californicus*). And, unless the La Brea blackbird (*Pandanaris convexa*) was more tightly adapted to commensal life with large mammals than any modern New World icterid (*21*), it is difficult to see that late Pleistocene mammal extinctions could have caused the demise of this bird. With one possible exception, then, none of the ten extinct late Pleistocene North American avian genera can be considered to have been ecologically dependent upon those mammals which disappeared at the end of the Pleistocene.

The argument that these birds were exterminated as a result of direct human predation places too great a burden on the overkill hypothesis, since that hypothesis is dependent upon the concept of big game hunters as the mechanism of extinction. If early North American human populations hunted an array of birds as diverse as those which became extinct at the end of the Pleistocene in such numbers as to cause their extinction, then these people could not have been dependent upon big game to the degree required by the overkill hypothesis. Either early North American human populations were big game hunters, and therefore could not have been the direct cause of the extinction of ten genera of birds, or they preyed upon birds, in which case their subsistence base would have been broader than the overkill hypothesis can accommodate.

In sum, during the last few thousand years of the North American Pleistocene, as many as 32 genera of mammals and ten genera of birds became extinct. For both mammals and birds, about half of all Pleistocene generic extinctions occurred during this narrow time interval. This episode of extinction affected animals ranging from blackbirds and pocket gophers to teratorns and mammoths, a range of variation that is too great to be accounted for by the hypothesis that terminal Pleistocene extinctions in North America were caused by human predation.

Table 2. Extinct avian genera from Rancho La Brea units 10, 28, 36, 37, and A. [Data from (*11*)]

Genus	Rancho La Brea unit
Ciconia	10(?), 36, A
Anabernicula	28(?), 36
Teratornis	10, 28(?), 36, A
Spizaetus	10, A
Morphnus	10
Wetmoregyps	A
Neophrontops	10, 36, A
Neogyps	10, A
Parapavo	10, 28(?), 36, A
Ectopistes	36
Pandanaris	A

DONALD K. GRAYSON
Department of Anthropology,
University of Washington, Seattle 98195

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8. Following Martin (*1*–*5*), I use the term "extinct" to refer to any taxon which existed in North America (the United States and Canada) at one time, but which today is extirpated or which is found only in tropical America or in the Old World. As did Martin, I restrict my examination to the generic level.
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23. I thank C. M. Aikens, P. Brodkorb, R. C. Dunnell, H. Howard, A. Krieger, P. S. Martin, C. Maser, P. Mehringer, Jr., and C. A. Reed for critical comments on early drafts of this manuscript. I especially thank P. S. Martin for stimulating discussions concerning Pleistocene extinctions.

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Regeneration of Oligodendroglia During Recovery from Demyelinating Disease

Abstract. *Infection of mice with the JHM strain of mouse hepatitis virus causes demyelination as a result of a cytolytic infection of oligodendroglia. In recovery, animals show remyelination, which could result either from surviving oligodendrocytes extending their territory or by generation of new oligodendroglia. Electron microscopic autoradiographic studies with* ^{3}*H-labeled thymidine demonstrate that the cells associated with remyelination are newly generated oligodendroglia.*

Demyelination in the central nervous system (CNS), the basic pathology of diseases like multiple sclerosis, can result from injury to oligodendroglial cells or to the myelin sheaths they maintain (*1, 2*). In a number of experimental models of demyelinating disease (*2–4*), recovery is associated with remyelination, a process that can occur in the face of local destruction of substantial numbers of oligodendroglia (*5, 6*). At least two mechanisms may be important in the process of remyelination. First, surviving oligodendroglia at the periphery of the lesion could expand their territory by extending processes into demyelinated regions to remyelinate the denuded axons. Second, cells in the oligodendroglial line (*7*) could undergo compensatory cellular proliferation. This study was designed to test the hypothesis that some of the oligodendroglia active in remyelination are newly generated cells.

Demyelination was produced in 4-week-old Swiss mice by intracerebral inoculation of a 10 percent suspension of suckling mouse brain containing one mean lethal dose (LD_{50}) of JHM virus (*8*) which is a neurotropic strain of mouse hepatitis virus (MHV), an enveloped, RNA corona virus. Control mice were similarly inoculated with a suspension of normal suckling mouse brain. In JHM infection, demyelination seems to result from a direct lytic effect of the virus on oligodendroglia (*9*). Multifocal demyelination is first apparent on day 3 after inoculation of the JHM virus on day 0. This pathological process is associated with death of oligodendrocytes and local inflammation. Approximately 50 percent of the mice die between days 7 and 12. By the end of the second week, active demyelination is no longer apparent. Mice surviving to the third week after inoculation show evidence of remyelination, and, at the end of 3 months, demyelinated areas are difficult to detect (*4*). In this study, [^{3}H]thymidine light- and electron-microscopic autoradiography was used to identify and characterize newly generated cells in the areas of remyelination.

Mice surviving the acute infection and control mice were given intraperitoneal injections of the DNA precursor, [^{3}H]-thymidine (specific activity 40.2 c/mmole). To cumulatively label proliferating cells (*10, 11*), two dosage schedules were used: 6 μc/g every 12 hours or 2 μc/g every 8 hours from day 13 through day 19 after inoculation. The spinal cords of experimental and control animals, fixed by perfusion at 21, 28, 35, and 49 days after inoculation, were prepared for light- and electron-microscopic autoradiography (*12*).

At each stage examined, lesions within the white matter of the spinal cord were evident. In areas of remyelination, silver grains indicating the incorporation of [^{3}H]thymidine were present in the emulsion overlying the nuclei of four types of cells: oligodendroglia (Fig. 1a), astroglia, inflammatory cells, and endothelial cells. Oligodendroglia were identified by their round nuclei containing clumps of heterochromatin, their dense cytoplasm containing many free polyribosomes, and microtubules (Fig. 1c) (*2, 7, 13*). Labeled oligodendrocytes were conspicuous in and adjacent to areas of active remyelination (Fig. 1b), but they were rarely seen

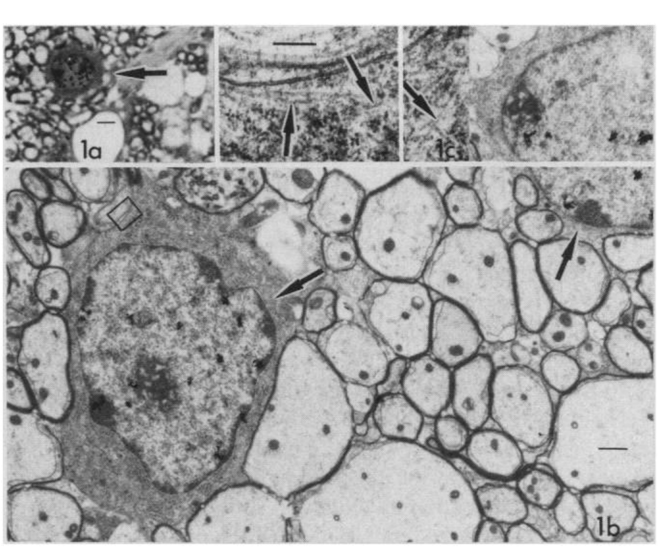

Fig. 1. (a) Light-microscopic autoradiograph of a heavily labeled oligodendrocyte (arrow) at the edge of a demyelinated area taken 28 days after inoculation. Scale, 5 μm. (b) Electron-microscopic autoradiograph of two oligodendrocytes (arrows) in a remyelinating area 28 days after inoculation. Both cells are heavily labeled as indicated by the silver grains scattered over their nuclei. Scale, 1 μm (lower right). The boxed area is enlarged in (c). (c) Portion of cytoplasm of oligodendrocyte shown in (b) illustrating microtubules (arrows), which help to identify this cell as an oligodendrocyte. Scale, 0.25 μm.