

Extinction of Birds in the Late Pleistocene of North America

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AT THE END OF THE PLEISTOCENE North American birds experienced more extinctions than any other group of organisms except the large mammals. These extinct forms included spectacular species, such as giant teratorns with wingspans of up to sixteen feet, and a variety of cathartid vultures, accipitrid vultures, hawks, and eagles. Birds are less often preserved in continental deposits than mammals, and the Pleistocene is no exception. While the fossil record of large mammalian genera has been relatively stable taxonomically over the past two decades, that of the Pleistocene avifauna has not. Descriptions of new faunas and revisions of old ones are changing its character.

To emphasize rarity of late Pleistocene extinction among small mammals, Martin (this volume, Tables 15.1 and 15.2) groups mammals into "large" (>44 kg) and "small" (<44 kg) categories. By this criterion, all extinct and living late Pleistocene birds are "small," and thus the 44-kg limit is not useful for North American birds. By avian standards the majority of extinct Pleistocene birds are rather large to very large. Late Pleistocene extinction affected flesh-eating birds, particularly carrion feeders, to a greater extent than the carnivorous mammals. Extinction in late Pleistocene mammals involved mainly large forms ("megafauna"), especially large herbivores such as ground sloths, mammoths, mastodons, horses, and camels. Unlike large mammals, the avian losses typically are only a small fraction of the total bird fauna known from any given late Pleistocene locality. The differences between mammalian and avian extinction suggest different causal mechanisms for each group. How are avian extinctions to be explained?

Synonymy and Chronology

In his *Catalogue of Fossil Birds*, Brodkorb (1963, 1964, 1967, 1971, 1978) listed a total of twenty-eight extinct genera (Table 21.1) from the Pleistocene in North America north of Mexico and excluding the West Indies. Certain of these genera are now considered invalid. Others have not been subjected to rigorous osteological comparisons, and may well prove to be synonymous with living genera. Because of many unresolved problems in the systematics of Pleistocene birds, a discussion of each extinct species is premature. We consider only extinct genera of birds, facilitating comparisons with generic extinctions in mammals.

We generally omit citations for references readily obtainable in the species account in Brodkorb's catalogue. Describers' names will be provided only for those genera described from fossils. Taxonomic judgments are Steadman's. Some genera in Table 21.1 may be eliminated from any discussion of late Pleistocene extinction. The supposed extinct heron, *Palaeophox* McCoy, was based on two specimens, one of which has been assigned to the living bittern *Botaurus lentiginosus*, and the other to the living barn owl, *Tyto alba* (Olson 1974a). *Brantadorna* Howard and *Titanis* Brodkorb apparently represent mid- or early Pleistocene extinctions, *Brantadorna* being known only from the Irvingtonian Vallecito Creek fauna, California, and *Titanis* from two sites in Florida, Santa Fe IB (Blancan) and Inglis IA (Irvingtonian). The flightless duck of the Pacific coast, *Chendytes* L. Miller, survived the Pleistocene to become extinct in the Holocene, the only case of its kind. Extinctions of historic time include the formerly widespread passenger pigeon, *Ectopistes*, and the Carolina parakeet, *Conuropsis*.

The supposed occurrence in North America of the eagle, *Hypomorphnus*, was based originally on the proximal end of the tarsometatarsus and a furcular symphysis from Fossil Lake, Oregon, described as *Aquila sodalis* by Shufeldt (1891). These specimens were restudied by Howard (1946), who found the furcular fragment to be from a different eagle than the tarsometatarsal bit, which she tentatively referred to *Hypomorphnus*, a genus now generally synonymized with *Buteogallus* (Blake 1977). In light of the poor quality of the fossils and the unsettled nature of generic level systematics of large accipitrids, we discuss them no further.

Neortyx Holman is known from three elements (nine total specimens) from Reddick and Haile XIB, two Rancholabrean sites in Florida. Another quail, *Colinus*, occurs in each of these faunas, and in great abundance at Reddick. *Neortyx* is within the size range of *Colinus*, a genus that is very similar osteologically to the closely related genera *Callipepla*, *Lophortyx*, and *Oreortyx*, for which Holman (1961) had few comparative specimens. At present the validity of *Neortyx* is uncertain.

Agriocharis and *Parapavo* L. Miller are now regarded as congeneric with the living turkey *Meleagris* (Steadman 1980). Whatever the status of *Creccoides* Shufeldt (see Olson 1977), the Blanco fauna of Texas is now considered to be Pliocene in age. *Aramides*, the genus of living neotropical wood-rails, has been reported from the late

Table 21.1. Extinct Genera of North American Pleistocene Birds,
As Listed in Brodkorb's Catalogue of Fossil Birds

S = a genus believed to be synonymous with a living genus; EP = extinction in the early Pleistocene or Pliocene; H = extinction in the Holocene; see text for details.

Family	Genus	Family	Genus
Phoenicopteridae	<i>Phoenicopterus</i>	Phasianidae	<i>Neortyx</i> —S
Ardeidae	<i>Palaeophox</i> —S		<i>Agriocharis</i> —S
Ciconiidae	<i>Ciconia</i>		<i>Parapavo</i> —S
Anatidae	<i>Anabernicula</i>	Rallidae	<i>Creccoides</i> —EP
	<i>Brantadorna</i> —EP		<i>Aramides</i> —S
	<i>Chendytes</i> —H	Phorusracidae	<i>Titanis</i> —EP
Vulturidae	<i>Breagyps</i>	Charadriidae	<i>Dorypaltus</i>
Teratomithidae	<i>Teratornis</i>	Columbidae	<i>Ectopistes</i> —H
	<i>Cathartornis</i>	Corvidae	<i>Protocitta</i>
Accipitridae	<i>Hypomorphnus</i> —S		<i>Henocitta</i>
	<i>Spizaetus</i>	Icteridae	<i>Cremaster</i>
	<i>Morphnus</i>		<i>Pandanans</i>
	<i>Wetmoregyps</i>		<i>Pyelorchampus</i>
	<i>Neophrontops</i>		
	<i>Neogyps</i>		

Pleistocene Seminole Field fauna of Florida; Olson (1974b) has shown that the two specimens involved are of the living *Rallus elegans*. The remaining seventeen genera of extinct birds in Table 21.1 appear to be more defensible taxonomically. All are late Pleistocene in age and are worthy of further consideration in interpreting late Pleistocene extinction.

Avian Extinctions

Of the nineteen late Pleistocene extinct genera, ten are known from the Rancho La Brea tar pits (Table 21.2), in deposits that postdate the last interglacial and lie within range of ^{14}C dating (see Marcus and Berger, this volume). P. Martin (1958, p. 403) proposed that the extinct birds of the late Pleistocene are mostly scavengers or commensals of the mammalian megafauna. We pursue this approach in more detail and find that the loss of many if not all extinct genera of late Pleistocene birds can be attributed to ecological dependencies on large mammals. Other possible explanations include climatic change, climatically induced range contractions, direct human predation, or stochastic turnover.

Table 21.2. Extinct Late Pleistocene Genera of North American Birds

*Indicates a genus that survives today outside North America; Brackets [] indicate a genus whose status has been questioned; R = occurrence at Rancho La Brea; see text for details.

Family	Genus	Common Name
Phoenicopteridae	* <i>Phoenicopterus</i>	flamingo
Ciconiidae	* <i>Ciconia</i>	stork—R
Anatidae	<i>Anabernicula</i>	shelduck
Vulturidae	<i>Breagyps</i>	condor—R
Teratomithidae	<i>Teratomis</i>	teratom—R
	<i>Cathartomis</i>	teratom—R
Accipitridae	* <i>[Spizaetus]</i>	hawk-eagle—R
	<i>Amplibuteo</i>	eagle—R
	(formerly <i>Morphnus</i>)	
	<i>Wetmoregyps</i>	"walking-eagle"—R
	<i>Neophrontops</i>	Old World Vulture—R
	<i>Neogyps</i>	Old World Vulture—R
Falconidae	* <i>Milvago</i>	caracara
Charadriidae	<i>[Dorypaltus]</i>	lapwing
Burhinidae	* <i>Burhinus</i>	thick-knee
Corvidae	<i>[Protocitta]</i>	jay
	<i>[Henocitta]</i>	jay
Icteridae	<i>[Cremaster]</i>	hangnest
	<i>[Pandanus]</i>	cowbird—R
	<i>[Pyelothampus]</i>	cowbird

The flamingo, *Phoenicopterus*, is known from deposits of two playa lakes (Fossil Lake, Oregon, and Manix Lake, California), the latter dating to the late Pleistocene. The nearest living populations of flamingos are those of *P. ruber* in the Caribbean region, where they breed locally in widely scattered places, suggesting refugia from human interference. Flamingos are not restricted to tropical climates, as shown by the modern range of *P. ruber* in southern Europe and Asia, and *P. chilensis* in southernmost South America. They are not scavengers. If the Manix Lake flamingo bred in North America, it probably inhabited saline playas of the Great Basin and Mohave deserts at times when they held shallow plankton-rich lakes. The intrusion of human hunters could have fatally disrupted these birds. On their breeding grounds flamingos are extremely vulnerable to nesting site disturbance (Brown 1959). With the arrival of prehistoric people nest robbing and disturbance of nesting birds could have been sufficient to cause a major contraction in the breeding range of American flamingos.

The stork, *Ciconia*, disappeared in the late Pleistocene of North America where it is recorded from California, Idaho, and Florida. Living storks often pursue small prey, as Grayson (1977) notes; others are well known for carrion feeding, e.g. the marabou, *Leptoptilos crumeniferus*, (Kahl 1966) and the woolly-necked stork, *Ciconia (Dissoura) episcopus* (see Mackworth-Praed and Grant 1962, 1970). Some commensal or scavenging role may be suggested in the case of North American storks (see fig. 21.1), including Cuba, where Pleistocene scavengers would have found large carrion in the form of endemic ground sloths and giant tortoises.

The shelduck, *Anabernicula* Ross, which occurs in the late Pleistocene of Oregon, California, Nevada, New Mexico, and Texas, is the only known case of extinction of an anatid genus in the late Pleistocene, evidently close to the time of megafaunal extinction. Migratory and wide ranging birds such as ducks and geese seem especially implausible candidates for extinction by climatic change. A scavenging or commensal niche can also be ruled out in the absence of any modern analogue, and we are left with the bare suggestion of prehistoric human impact. However, in reviewing the habits of living species of the Tribe Tadornini we find nothing that clearly suggests any special vulnerability to human predation.

The only other anatid genus to become extinct in prehistoric time was the flightless duck, *Chendytes*, which occurs abundantly in archaeological sites. According to Morejohn (1976, p. 210), "overharvest by aboriginal man was probably the principal factor contributing to the extinction of this species." *Chendytes* is unique among North American genera of extinct Pleistocene mammals and birds in being highly visible in certain archaeological sites.

The group suffering the greatest late Pleistocene extinction was the raptorial birds—the condors, teratorns, eagles, accipitrid vultures, and caracaras. They make up nine of the nineteen genera in Table 21.2. While feathers may have been sought, extermination by hunting is unlikely. The extinct condor, *Breagyps* L. Miller and Howard, is recorded from three late Pleistocene sites: Rancho La Brea, California; Smith Creek Cave, Nevada; and Shelter Cave, New Mexico (Howard 1971). The huge teratorns include *Teratornis* L. Miller and *Cathartornis* L. Miller. *Cathartornis* occurs only at Rancho La Brea, while *Teratornis* is more widespread. *Teratornis merriami* is known from three late Pleistocene faunas in California (Rancho La Brea, McKittrick, and Carpinteria), as well as the Seminole Field and Bradenton faunas in Florida. Webb (1974) assigns a latest Pleistocene age to Seminole Field, while putting Bradenton very early in the Rancholabrean land mammal age. A related species, *Teratornis incredibilis*, from the late Pleistocene of Smith Creek Cave, Nevada, was the largest known North American flying bird. The hawk-eagles, *Spizaetus*, are recorded from a variety of western late Pleistocene records for the accipitrid "Old World" vultures, *Neophrontops* L. Miller and Smith Creek Cave, Nevada; and Howell's Ridge Cave, New Mexico. *Morphnus woodwardi* is an eagle from Rancho La Brea that Campbell (1979) has assigned to an otherwise South American extinct genus, *Amplibuteo* Campbell. The long-legged "walking eagle," *Wetmoregyps* L. Miller, is known from Rancho La Brea and Carpinteria. Late Pleistocene records for the accipitrid "Old World" vultures, *Neophrontops* L. Miller and *Neogyps* L. Miller, include Rancho La Brea, McKittrick, and Carpinteria, with *Neophrontops* also at Dark Canyon Cave, New Mexico (Howard 1971), and *Neogyps* at Smith Creek Cave, Nevada. A caracara, *Milvago*, is known only from two late Pleistocene faunas in Florida—Itchtucknee River and Arredondo IIA (Campbell 1980).

The extinction of scavengers, such as *Breagyps*, *Teratornis*, *Cathartornis*, *Neophrontops*, and *Neogyps*, can be attributed to their dependency on the megafauna for a diverse and abundant supply of carrion. Presumably some preyed as well on very young, weak, or sick animals. For analogies one turns to those parts of Africa that will sustain a diverse megafauna. According to Houston (1975, p. 55), "Africa now supports more species of accipitrid, or Old World vultures than any other continent, up to seven species being found in any one area." It is not unusual to see five species feeding from

the same carcass. One group with long, bare necks reaches far inside a carcass to slice with its sharp bill and withdraw slippery meat on a barbed tongue. These include the griffins, *Gyps africanus* and *G. ruepellii*. A second group that does not gather in large numbers has deep, powerful bills (like those of teratorns) to feed on tougher parts of the carcass such as skin and tendons; these include the lappet-faced vulture, *Torgos tracheliotus*, and the white-headed vulture, *Trigonoceps occipitalis*. Houston (1975) notes a third group of small, thin-billed vultures that takes lizards, insects, and dung as well as carrion and is also partial to village rubbish heaps. The hooded and Egyptian vultures, *Necrosyrtes monachus* and *Neophron percopterus*, belong here. On a strategy of its own, the lammergeyer (*Gypaetus barbatus*) ingests the shattered remains of large limb bones, carcasses, or even tortoises it has dropped from a height in mountain canyons.

In Natal the lappet-faced and white-headed vultures occur in game country; with the elimination of the large native mammals they disappear (Clancey 1964). Boshoff and Vernon (1980) have postulated that the reduced numbers of Cape vultures (*Gyps coprotheres*) in the Cape Province of South Africa is due to the drastic decline of game herds, as well as recent changes in cattle ranching. It seems logical to view the rapid extinction of most of North America's megafauna as having had a comparable effect on New World scavenging birds.

Many hawks and eagles that are generally considered predatory may also feed on carrion. For Africa, Brown (1970, p. 296) lists four eagles (*Aquila rapax*, *A. heliaca*, *Haliaeetus vocifer*, *Terathopius ecaudatus*), four hawks (*Buteo* spp.), and a kite (*Milvus migrans*) as eaters of the carrion of mammals weighing more than 10 kg. In India, Ali and Ripley (1968, pp. 227, 231, 253, 274-279, 286, 291, 325) note occasional to regular carrion feeding in two kites (*Milvus migrans*, *Haliastur indus*), a hawk (*Buteo rufinus*), six eagles (*Aquila chrysaetos*, *A. heliaca*, *A. rapax*, *A. nipalensis*, *Haliaeetus albicilla*, *H. leucoryphus*), and a harrier (*Circus aeruginosus*).

The Rancho La Brea tar deposits have yielded an abundance of scavenging birds. They match the large numbers of bones of scavenging mammals found there, such as the dire wolf (*Canis dirus*). Apparently the niche for all sorts of scavengers was expanded during the late Pleistocene. If the African analogy holds, it seems obvious that *Breagyps*, *Teratornis*, *Cathartornis*, *Neophrontops*, and *Neogyps* shared carrion-feeding duties at Rancho La Brea with other scavengers that survived, such as *Gymnogyps*, *Cathartes*, *Coragyps*, *Aquila*, *Polyborus*, and *Corvus* (fig. 21.1). Most surviving raptors, eagles as well as vultures, declined with the extinction of other guild members. The only scavenger whose bones increase at Rancho La Brea after the loss of the large mammals and birds is the turkey vulture, *Cathartes aura* (Howard 1962), a consumer of small carrion.

In addition to vultures we propose other raptorial genera as possible obligate scavengers of the Pleistocene megafauna. Grayson (1977, p. 692) has noted that *Wetmoregyps*, *Morphnus* (= *Amplibuteo*), and *Spizaetus* "most likely relied primarily upon small vertebrates for food, as do the extant congeneric relatives of two of them." However, *Wetmoregyps* is a long-legged "eagle" of unknown ecology; it may well have been a scavenger. The ecology of the extinct genus *Amplibuteo* is also highly speculative at present. *Spizaetus* is tropical in its modern range and is not known to scavenge. We are reluctant to consider any environmental change as sufficient to explain the retreat of *Spizaetus* into the truly tropical parts of Mexico, where it occupies regions dominated by *Ficus*, *Enterolobium*, *Inga*, *Bursera*, and other tropical trees. No tropical plants have been found in the rich paleoflora of Rancho La Brea (Johnson 1977) or at Smith Creek Cave, Nevada, where Pleistocene *Spizaetus*, as well as *Breagyps*, *Teratornis*, and *Neogyps* have been reported. The associated late Pleistocene fossil plant record at these localities is richer in species of northern rather than southern distribution. Thompson (1978) has shown that the late Pleistocene vegetation in the now treeless area of Smith Creek Cave prior to faunal extinction was a coniferous forest or woodland dominated by bristlecone pine (*Pinus longaeva*).

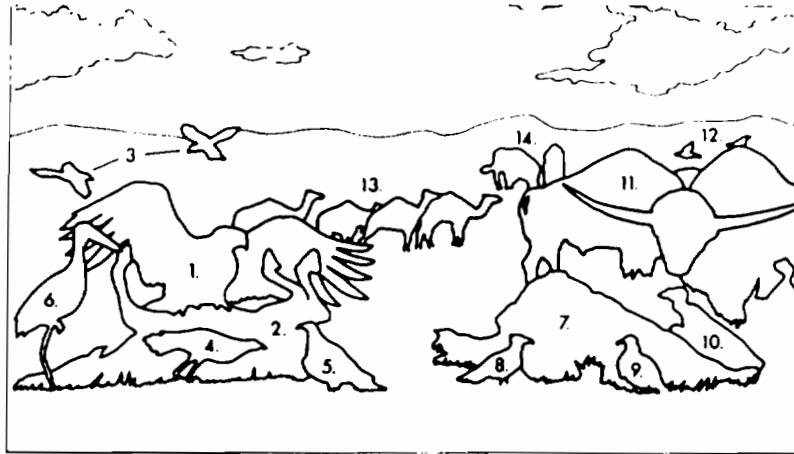


Figure 21.1. A scene from the late Pleistocene of western North America; * = extinct genus or species. On the left, (1) a teratom, *Teratomis merriami*, stands upon the carcass of a (2) freshly dead horse, *Equus* sp. The teratom has just scared away (3) two magpies (*Pica pica*) that are flying overhead. Below the teratom, a (4) long-legged eagle, *Wetmoregyps daggetti*, rushes up to rip a piece of flesh from the carcass. To the right of *Wetmoregyps*, (5) a golden eagle (*Aquila chrysaetos*) pauses to keep an eye on the teratom before resuming its feeding activities. To the left of the teratom, (6) a stork, *Ciconia maltha*, awaits its chance to run up to the dead horse and grab a piece of meat or entrails that has been exposed by the teratom or the eagles. On the right side of the scene is another dead horse (7). This animal has been dead for about a week. The teratoms and eagles have already removed most of the entrails, as well as much of the meat. On the left is an (8) accipitrid vulture, *Neophrontops americanus*, that is keeping its distance from the other scavengers as it looks for an opportunity to feed upon some soft, easy-to-tear flesh that has been exposed. To the right of *Neophrontops* is a (9) black vulture, *Coragyps atratus*, and (10) a large condor *Breagyps clarki*. The large size of *Breagyps* allows it to feed deeply within the body cavity of the horse. Behind *Breagyps* are several (11) long-horned bison, *Bison latifrons*, accompanied by two commensal (12) cowbirds, *Pandanaris convexa*. In the center background, a small herd of (13) camels, *Camelops hesternus*, and two (14) mammoths, *Mammuthus jeffersoni*, are moving through the grasslands. Sooner or later, they too will provide carrion for the avian scavengers.

It seems that Pleistocene populations of *Spizaetus* transcended their modern geographic and ecological range. Whether the extinct populations would have also changed their behavior cannot be determined. The remarkable decline of golden eagles (*Aquila chrysaetos*) and bald eagles (*Haliaeetus leucocephalus*) that accompanied extinction of the teratoms at Rancho La Brea (Howard 1962) suggests that at least locally a number of falconiform birds may have found more opportunity as scavengers in the time

of the tar pit megafauna than afterwards. It is possible that *Spizaetus* shared in the generalized scavenging opportunity, one that allowed an extension of their range. All of this depends, of course, upon correct systematic assignment of the fossils currently placed in the genus *Spizaetus*.

Concerning extinction of *Milvago* in North America, Campbell stated (1980, p. 127) that "Many other factors may have been responsible for the extinction of *M. readei*, but the climatic and vegetational changes at the end of the Pleistocene that resulted in the loss of the dry savanna habitat in Florida were probably the most important." We suggest that extinction of large mammals may have been just as important in the North American loss of *Milvago*, a scavenger today confined to Costa Rica, Panama, and much of South America and known to associate with large herbivores. For example, Vuilleumier noted (1970, p. 3), "in Patagonia, *Milvago chimango* flocks are frequent near cattle and horses; I even saw one bird sitting on the flank of a lying horse, pecking from time to time at the skin, perhaps to eat ticks."

A cooling climate could certainly explain range shrinkage of larger raptorial birds that seasonally migrate south from higher latitudes. However, a climatic model that would propose the *complete* extinction of raptors, well known for their broad ecological amplitude, appears unpromising. At least within lower latitudes they appear to be independent of any particular climatic or vegetation type. If the loss of most large mammals drastically reduced the food supply for scavengers, a sequence of scavenger extinctions may be explained. Scavenging and commensal roles are mainly but not entirely the specialty of large raptorial birds. A few extinct genera of smaller birds, including some passerines, are ecologically dependent on large mammals.

Dorypaltus Brodkorb is known from four partial elements (eight total specimens) from the late Pleistocene sites of Arredondo IIA and Haile XIB, Florida. If *Dorypaltus* is indeed a lapwing, its generic distinction (as reported in Brodkorb 1959 and Ligon 1965) is not certain because comparisons were made with only two modern lapwings, the South American *Belonopterus chilensis* and the Eurasian *Vanellus vanellus*. Eight genera and eleven species of lapwings are resident in Africa (Peters 1934) where Mackworth-Praed (1962, 1970) reports that two African lapwings, the black-wing plover (*Stephanibyx melanopterus*) and blacksmith plover (*Hoplopterus armatus*), prefer grassy areas much used by cattle or large native mammals. In India the lapwing, *Vanellus vanellus*, often forages in "wet meadows or grazing land in proximity of cattle" (Ali and Ripley 1969, p. 211). Further speculations on the cause of extinction of *Dorypaltus* may be reserved until its status is clarified.

The thick-knee, *Burhinus*, is recorded from Dark Canyon Cave, New Mexico (Howard 1971), a locality tentatively dated at between 25,000 and 12,500 yr B.P. (Harris 1977), and the Sanborn Formation, Kansas, referred to the Sangamonian interglacial (Feduccia 1980). These fossils appear not to be very different from the living *B. bistratus*, which reaches its northern limit on the Gulf slope of eastern Mexico with one record from southern Texas (MacInnes and Chamberlain 1963). Feduccia emphasized that modern species of *Burhinus* are characteristic of arid or semiarid tropical areas, and concluded that the same must be true for the fossil species. However, the stone-curlew, *B. oedicephalus*, occurs in temperate Eurasia as far north as the British Isles, Germany, and Poland (Bannerman 1962, p. 28). The Dark Canyon Cave record may be associated with xeric pinyon-juniper woodlands (Van Devender and Spaulding 1979, Thompson et al. 1980) and a much cooler climate than any modern tropical savanna. Possibly the ecological tolerances of American *Burhinus* were broader in the Pleistocene. We found no traits of living *Burhinus* that would suggest an intimate ecological relationship with large mammals.

Late Pleistocene extinction in the largest avian order, the passerines, is limited to members of two families, the corvids and icterids. Loss within these groups is in accord with our dependency model; no other American perching birds are as intimately associated with large mammals.

Protocitta Brodkorb is a supposedly extinct genus of jay. It is known from the late Pleistocene faunas of Reddick and Haile XIB, Florida, and Miller's Cave, Texas, as well as several pre-Rancholabrean faunas. *Protocitta* is very similar, particularly in size (Brodkorb 1972), to living neotropical jays of the genera *Psilorhinus* and especially *Calocitta*. Another extinct jay, *Henocitta* Holman, is known only from a single distal end of a humerus that is insufficient to establish its status firmly. Holman (1959) stated that *Henocitta* is closest to *Psilorhinus*. In his extensive osteology of Pleistocene passerine birds, Hamon (1964) did not compare *Protocitta* and *Henocitta* to *Calocitta* or *Psilorhinus*. We feel that these comparisons should precede detailed ecological speculation. *Calocitta* lives today as far north as central Sonora, whereas *Psilorhinus* reaches its present northern limit in the lower Rio Grande Valley of Texas. The late Pleistocene occurrence of tropical jays in Florida and central Texas would not be surprising and would complement the record of jaguars, ocelots, and other presently "tropical" animals that once occupied this region (see Webb 1974).

If either *Protocitta* or *Henocitta* prove not to be synonymous with living neotropical jays, it is possible that they represent an autochthonous American development of the piapiac or magpie niche, one that collapsed in America with late Pleistocene extinction of large mammals. The piapiac, *Ptilostomus afer*, is a black, rather magpielike African corvid that feeds on insects in close association with large mammals, both wild and domestic (Rice 1963). In the case of American magpies (*Pica pica*), Linsdale (1937) noted that carrion served as their main animal food in winter on the High Plains of North America. Magpies became scarce after buffalo declined in historic time. Winter road kills as well as the spread of domestic livestock apparently restored their food supply and led to their present recovery.

The icterid *Cremaster* Brodkorb is known from only three elements (four total specimens) from Arredondo IIA and Haile XIB, Florida. Until compared to a large series of Mexican forms such as *Amblycercus holosericeus*, *Cassiculus melanicterus*, *Dives dives*, and *Icterus gularis*, one cannot safely regard *Cremaster* as an extinct genus. Two other extinct genera of icterids have been described. *Pandanaris* A. Miller is known from Reddick and Haile XIB, Florida, and Rancho La Brea, California. *Pyelorhamphus* A. Miller is from Shelter Cave, New Mexico, the source of a late Wisconsinan biota indirectly associated with the radiocarbon-dated dung of an extinct ground sloth (Thompson et al. 1980). Both *Pandanaris* and *Pyelorhamphus* are cowbirdlike forms that could prove to be congeneric with *Molothrus* (including *Tangavius*). Based on mandibles and rostra instead of only postcranial elements, these genera seem to have a stronger basis than *Cremaster*. As pointed out by P. Martin (1958, p. 403), the extinction of both *Pandanaris* and *Pyelorhamphus* can be explained by proposing a close commensal relationship between them and large Pleistocene herbivores; if not "cowbirds," perhaps they were "mastodont birds."

Aside from the piapiacs already mentioned, other passerine associates of large African mammals include the oxpeckers, *Buphagus* (Family Sturnidae), which are scab feeders, and drongos, *Dicrurus* (Family Dicruridae), which are insect eaters (Rice 1963). Thus it is possible to postulate that a variety of commensal relationships existed independently in the New World, as in Africa, only to be lost with the late Pleistocene disappearance of most American large mammals.

Discussion

Within the late Pleistocene avifauna, human impact may have been the direct cause of extinction only in the case of the flamingo and one anatid, *Chendytes*. The latter, a flightless scoter, survived the extinction of large herbivores presumably to succumb in the Holocene when the coastal Indians of California improved their watercraft to reach

the offshore islands where *Chendytes* bred. While details of even historic extinctions are poorly known, the passenger pigeon, *Ectopistes*, and Carolina parakeet, *Conuropsis*, are considered to have been victims of human impacts in historic time.

Grayson (1977) proposed to test the thesis of overkill by comparing the number of extinct birds with extinct mammals, regardless of size. He did this in an unusual way, dividing the number of late glacial extinct genera by the total number of known bird extinctions for the entire Pleistocene. Both birds and mammals yielded extinction ratios of just under 50 percent, which he took as discordant with an overkill model. Grayson's method obscures the fact that virtually all late Pleistocene mammalian extinctions are of large mammals, which is not the case earlier in the Pleistocene (see Martin this volume). Furthermore, unlike the large mammals, most late Pleistocene birds belong to living genera. For example, in the case of song birds, only five genera are listed as extinct, three icterids and two corvids (see Table 21.2) while fifty-one living genera have been reported (see Table 21.3). The late Pleistocene ratio is 10 percent, comparable to late Pleistocene avian extinction estimates of 15 percent previously obtained for Rancho La Brea (Howard 1962) and within the range noted in other late Pleistocene faunas in North America (Selander 1965). Had birds suffered as much extinction as did the *large mammals*, two thirds of the Wisconsin-age avifauna would be extinct.

Birds suffered more generic extinction within the Rancholabrean age than did the small mammals. We agree with Grayson (1977) that in most cases the avian extinctions in continental America are not to be attributed directly to human impact. At the same time we are impressed with the scavenging or commensal behavior that can be attributed to most of the genera listed in Table 21.2. Commensals or scavengers of large mammals are not known among the loons, grebes, gulls, grouse, shorebirds, and woodpeckers, all well represented in the Pleistocene fossil record (see Brodkorb 1963, 1964, 1967, 1971). None of these groups includes extinct genera. No generic extinction occurred among continental owls in the Pleistocene, to match that of the falconiform birds (Miller and de May 1942). We suggest that this is simply because owls, unlike vultures, do not, and did not, scavenge. There is a marked increase in owls and rodent-feeding hawks following megafaunal extinction at Rancho La Brea (Howard 1962; pits 37, 28, 10). This may mark a shift in mammalian biomass with an increase in mice and mouse-eaters after the ground sloths and mastodons departed.

If climate had played an important role in avian extinctions of the late Pleistocene, one might expect the relatively rich Pleistocene avifaunas of Europe to yield examples, in view of the severe climatic changes that occurred there. However, no generic extinctions of birds are known in Eurasia in the Pleistocene. *Pliogallus* Gaillard, a phasianid listed from the Pleistocene of Hungary in Brodkorb's catalogue, is now considered Pliocene in age. All other birds in the Pleistocene avifaunas of Eurasia are assigned to living genera.

In a few cases avian losses may reflect range contractions of subtropical genera still living in Mexico or southern Texas. In most it appears that late Pleistocene extinct birds fall into groups well known for their scavenging or commensal behaviors. The reason more birds than small mammals became extinct is that very few small mammals (only vampire bats) were ecologically dependent on the megafauna. Late Pleistocene extinct birds of North America constituted 10 to 20 percent of the known fossil genera, far too few to be comparable to the accompanying late Pleistocene megafaunal extinctions, which exceeded 60 percent. No other groups of organisms were appreciably involved in the extinctions.

The avifaunal losses lend no support to any particular causal theory advanced to explain the extinction of the large mammals. Whatever caused megafaunal extinction will indirectly explain known avian extinctions. As in the case of the extinction of mammalian

Table 21.3. Living Genera of Passerines Reported From North American Pleistocene Avifaunas, Derived From Brodkorb (1978)

Question mark indicates uncertainty about identification or age assignment (i.e. might be Holocene portion of a Pleistocene locality).

Family	Genus	Common Name	
Tyrannidae	<i>Sayornis</i>	phoebe	
	<i>Tyrannus</i>	kingbird	
	<i>Contopus</i>	pewee	
Alaudidae	<i>Empidonax</i>	empidonax flycatcher	
	<i>Eremophila</i>	lark	
Corvidae	<i>Gymnorhinus</i>	pinyon jay	
	<i>Aphelocoma</i>	jay	
	<i>Cyanocitta</i>	jay	
	<i>Perisoreus</i>	gray jay	
	<i>Pica</i>	maggie	
	<i>Nucifraga</i>	nutcracker	
	<i>Corvus</i>	crow, raven	
	<i>Parus?</i>	tit	
	Paridae	<i>Sitta</i>	nuthatch
	Sittidae	<i>Troglodytes</i>	wren
<i>Salpinctes</i>		wren	
Troglodytidae	<i>Campylorhynchus?</i>	cactus wren	
	<i>Cistothorus</i>	marsh wren	
	<i>Toxostoma</i>	thrasher	
	<i>Oreoscoptes</i>	sage thrasher	
	<i>Mimus</i>	mockingbird	
Muscicapidae	<i>Sialia</i>	bluebird	
	<i>Catharus</i>	thrush	
	<i>Turdus</i>	robin	
	<i>Chamaea</i>	wren-tit	
	<i>Bombycilla</i>	waxwing	
	<i>Lanius</i>	shrike	
	<i>Vireo</i>	vireo	
	<i>Mniotilta?</i>	warbler	
	<i>Geothlypis</i>	yellowthroat	
	<i>Pyrthuloxia</i>	cardinal	
Tanageridae	<i>Pheucticus</i>	grobeak	
	<i>Agelaius</i>	blackbird	
Icteridae	<i>Sturnella</i>	meadowlark	
	<i>Quiscalus</i>	grackle	
	<i>Euphagus</i>	blackbird	
	<i>Molothrus</i>	cowbird	
	<i>Dolichonyx</i>	bobolink	
	<i>Pipilo</i>	towhee	
Emberizidae	<i>Calamospiza</i>	lark bunting	
	<i>Passerculus</i>	savannah sparrow	
	<i>Ammodramus</i>	sparrow	
	<i>Pooecetes</i>	vesper sparrow	
	<i>Chondestes</i>	lark sparrow	
	<i>Amphispiza</i>	sparrow	
	<i>Spizella</i>	sparrow	
	<i>Junco</i>	junco	
	<i>Zonotrichia</i>	sparrow	
	<i>Calcarius?</i>	longspur	
	Passeridae	<i>Carduelis</i>	goldfinch
		<i>Carpodacus</i>	finch
<i>Coccothraustes</i>		evening grosbeak	
<i>Loxia</i>		crossbill	

predators, scavengers, or parasites, such as the sabertooth, extinct lion, dire wolf, and an extinct dung beetle, the avian losses appear to depend on the loss of large herbivores.

In terms of total fossil fauna, the extinction of Pleistocene birds is a minor exception to the view (Martin this volume) that small animals on the continent were unaffected by the late Pleistocene extinction phenomenon. Our conclusion can be falsified if future paleontological workers on this continent uncover many more extinct birds of late Pleistocene age, especially birds in groups that cannot be viewed as scavengers or commensals of the large mammals, or be regarded as easy prey for the prehistoric hunters. Bird extinction on oceanic islands is another matter (Cassels and Olson and James this volume).

Acknowledgments

Conversations on Pleistocene birds with Storrs L. Olson and Don K. Grayson and a critical review by Kenneth C. Parkes have been beneficial. Deborah Gaines and Debbie Rollman typed the manuscript. Figure 21.1 is by Lee M. Steadman.

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