

Avian influenza as the Cause of Late Pleistocene
Mammalian Megafaunal Extinctions in the Americas

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We attribute the Late Pleistocene extinction of many mammals in the Americas to an avian influenza virus that originated among waterfowl in Southeast Asia, was highly pathogenic to mammals but not necessarily contagious between them, and was transported by asymptomatic migratory birds to waters ingested by those mammals.

Abstract

We attribute Late Pleistocene mammalian extinctions in the Americas to an avian influenza virus originating in Southeast Asia. We hypothesize that an antigenic shift produced a viral strain that was asymptomatic in waterfowl but highly pathogenic to mammals though not necessarily contagious among them. Migratory American waterfowl sharing breeding grounds with Asian waterfowl transported the virus throughout the Americas. Mammals inhabiting regions with shallow bodies of water contaminated by infected migrating waterfowl were most vulnerable. A logistic regression of estimated level of water contamination, mass, and reproductive rate against extinction status for 383 species of mammals living in North America at the end of the Pleistocene supports this model. Some characteristics of the pathogen proposed for this model closely resemble reported characteristics of currently circulating strains of avian virus, suggesting an effective first line of defense against all avian viruses would be protection of sources of drinking water.

Introduction

None of the models proposed over the past half-century to explain the cause of the Late Pleistocene mammalian megafauna extinctions has led to broad consensus. Those models include *blitzkreig*, rapid over-hunting by immigrating humans; *sitzkreig*, fire use, habitat fragmentation, or exotic immigrants; *climate change*, leading to shifts of vegetation types in space and time, thereby disrupting previously cohesive mammal assemblages; *disruption of habitat maintenance* resulting from loss of key megaherbivores such as mammoths and mastodons; *hyperdisease* in which a contagious pathogen introduced by immigrant humans or their commensals was lethal to a broad range of mammals of large body size but not to humans, their commensals, or small mammals; and *low reproductive rates combined with hunting by humans* (1-3). The proposed model incorporates aspects of some of these models, identifies risk factors for extinction due to pathogenic avian influenza viruses, and analyzes the expected effects of these factors on extinction status for 383 mammal species living in North America in the late Pleistocene.

All known influenza A virus subtypes appear to have originated from birds (4), with new strains most commonly emerging in Southeast Asia (5). We propose that region as the source of the strain causing the Late Pleistocene mammalian extinctions 10-12,000 years ago. Waterfowl in the Anseriformes (ducks, geese and others) and Charadriiformes (sandpipers, plovers, gulls, and others) are common reservoirs of avian influenzas (6). Avian influenza viruses may become asymptomatic and genetically stable in birds, and an individual bird in some species may be infected by more than one strain of virus (coinfection) (7). Pigs, which occur naturally over wide areas of Europe and

Asia, (8) can acquire influenza viruses from birds and occasionally from humans (9). Coinfection in birds or pigs may result in reassortment in which genes in the internal RNA segments are replaced by genes from another source. This antigenic shift can produce viruses highly pathogenic to various birds and mammals, including humans (4). Reassortment is an uncommon event but presumably becomes more likely when the population density of host species is high. Avian influenzas usually are not highly contagious between mammals (10), although apparently contagious forms emerged several times among human populations during the past century (9).

Maintenance of viral reservoirs and transmission across generations of domestic ducks in southern China has occurred in ponds shared by different generations (11), suggesting that viral reservoirs could be maintained on waterfowl breeding grounds at high latitudes where viruses are shed in water via feces (4, 11, 12). Viruses remain viable in water for some time (11, 13), particularly when the water is cold (14). Transmission of avian viruses among birds, pigs, and humans could occur by ingestion of contaminated water (9).

The assumption that influenza virus strains responsible for the Late Pleistocene extinctions were not highly contagious among mammals is a critical component of our model. Pathogens that depend on host-to-host transmission increase their likelihood of being passed to new hosts by evolving reduced virulence thereby gaining time for offspring to reach a new host, whereas pathogens transmitted by water or arthropods can sustain relatively high levels of virulence without losing evolutionary fitness (15). A virus asymptomatic in birds but pathogenic to mammals if transmitted through water therefore might remain in a static virulent form in its bird reservoir for many years.

In North America migration of waterfowl especially in mid-continent is facilitated by numerous small lakes (prairie potholes) created by the melting of large masses of buried glacial ice left behind by retreating glaciers (16). These bodies of water are situated on a major flyway in North America and are used as stopover areas during migration of waterfowl (Fig. 1). This region is one of the most important waterfowl breeding grounds in the world (17). We assume many of these pools or small lakes in the Late Pleistocene became contaminated with pathogenic avian influenza viruses. Similarly, in South America, the Pantanal wetlands have an unusually high diversity of birds, and some species migrate between the Americas as well as throughout South America (18). Birds wintering in these wetlands and breeding in North America may have contributed to widespread dispersal of the influenza virus in South America. Local dispersal of the virus within both continents might have been augmented by nonmigratory waterfowl that became infected during seasonal residence of infected migratory waterfowl.

Asiatic migratory birds such as the Bar-tailed Godwit have breeding grounds that overlap those of North American species in Alaska (19). Similarly, the breeding grounds of the Sandhill Crane and various other North American winter residents include northeastern Siberia (20). Infected migratory waterfowl from Asia would have been well positioned to transfer viruses to North American species. Transfer of viruses between aquatic species apparently takes place via feces released into water. Interspecific mixing of large numbers of aquatic birds at stopover sites during migration provides opportunity for lateral transmission of viruses among adults (21). Vertical transmission of viruses (adults to young) may occur primarily on the breeding grounds (14).

The proposed transfer of viruses occurred between Asiatic and American waterfowl in the Late Pleistocene, perhaps aided by the existence of a broad land bridge between Asia and North America exposed during the low sea level of glacial periods. Subsequent spread of the virus to other birds in the Americas and eastern Eurasia may have been rapid as occurred with the West Nile Virus in 1999-2003 (22). Mammals in the Americas were exposed to viruses in water contaminated by migrating aquatic birds. Stable viral reservoirs in birds led to repeated contamination of bodies of water, preventing recovery of initially decimated mammal populations.

This hypothesis predicts the highest extinction rates for North American mammals would occur for species relying on drinking water contaminated by feces of migratory waterfowl. The model of overkill by humans, however, predicts a strong positive relationship between body mass of mammals and extinction, based primarily on the assumption that human hunters preferentially chose the largest prey available (23). Both models predict that mammals with low reproductive rates that limited their capacity to recover from episodes of high mortality would have been most vulnerable to extinction. We tested both models using a data set of terrestrial mammals present in North America during the Late Pleistocene (Table S1).

Species were categorized as extinct or extant after the Pleistocene, and ranked 1-3 according to increasing levels of estimated exposure to viral contamination. A logistic regression model using water contamination level and reproductive rate as predictors and extinction as the response variable resulted in strong measures of association (90.7% rate of concordance, $d = 0.82$, $\text{Tau} = 0.25$). The probability of extinction increases with exposure to contaminated water, and decreases with increasing reproductive rate. A

second model was fit using log mass and log reproductive rate as predictors (90.7% rate of concordance, $d = 0.82$, $\text{Tau} = 0.25$). These results support both scenarios identically.

There is a strong correlation between log mass and log reproductive rate ($r = -0.816$) because large mammals breed more slowly than small ones. Large mammals often live in open habitats and drink from bodies of water that would be accessible to infected migratory waterfowl. A third logistic regression model using all three factors significantly improves on each of the models above (92.5% concordance, $d = 0.85$, $\text{Tau} = 0.27$) (Fig. 2). Pairwise comparisons of probability of extinction for the three levels of water contamination show that probability of extinction (diagonal lines in Fig. 2) increases from moderate to high contamination, with even greater increase from low to high contamination .

The viral model and the overkill model both predict a strong positive relationship between body size and probability of extinction (24), but they make different predictions for mammals weighing more than 10 kg and producing no more than 2 young/year. The overkill model predicts increase in extinction rates with mass alone, whereas the viral model predicts differences between contamination categories. Survival of several large-bodied mammals that probably were hunted is better explained by the waterborne virus model than by the overkill model. Survival of modern plains bison and pronghorns, presumably exposed to contaminated water in most of their ranges, may reflect survival of populations living at high elevations in the Rocky Mountains (25), far from contaminated water. Similarly, alpine species such as mountain sheep and mountain goats survived with the exception of one species , as did large forest-dwelling mammals (elk, moose and white-tailed deer), whose water sources would have been less subject to

contamination. Eventual disappearance of the influenza strain from the migratory waterfowl viral reservoir would have permitted repopulation of the prairie regions of North America by megafauna survivors.

Large extinct carnivores such as the American lion, American cheetah, dire wolf, and sabertooth cat that specialized on plains animals would have been doubly vulnerable due to consumption of contaminated water and loss of prey. In contrast, widespread omnivorous species (American black bear, grizzly bear), large carnivores adept at prey-switching (gray wolf), and those that hunted forest prey (mountain lion, jaguar) did not go extinct. In the arctic, polar bears may have escaped the virus due to winter hibernation and foraging on pack ice during the summer, thus having little contact with breeding waterfowl. The range of the muskox includes arctic islands, with high desert habitat presumably unsuited for waterfowl reproduction. Extirpated island populations could have been replaced by animals traveling across ice (26). Caribou often occur in regions of abundant bodies of water presumably reducing viral exposure through dilution of the virus. Long-distance migratory movements of up to 5000 km/yr (25) would allow eventual replacement of extirpated populations.

The proposed model to explain megafaunal extinctions requires no direct interactions between megafauna and humans, distinguishing it from almost all previous models. It is most similar to that proposed by Johnson (2) who emphasized the importance of life history traits (particularly reproductive rates) and ecology (habitats) to account for the survival of some species. Megafaunal extinctions in Johnson's model, however, are attributed to hunting by humans, whereas the present model invokes the emergence of a virus highly pathogenic to mammals dispersed widely by asymptomatic

birds. Johnson's model assumes forest habitats provided protection from human hunters, whereas our model suggests those environments provided protection from the virus due to absence of water sources frequently used by migratory waterfowl.

Stevens, et al. (27), commenting on the current spread of H5N1, suggested that contaminated water may be involved in its transmission between birds and humans, but did not consider that the most likely route. In contrast, the model of Late Pleistocene extinctions presented here postulates contaminated drinking water as the primary mode of transmission. Recent occurrences of H5N1 influenza infections in humans between members of the same family have been explained as likely resulting from human-to-human transmission (28) but see (29). We think it more likely all members of a family consumed contaminated water from the same source, and therefore presented identical H5N1 strains. Such an occurrence seems likely in rural areas where drinking water is obtained locally from unprotected surface water sources. Our model suggests that protection of drinking water sources and assurance of water purity would reduce exposure to all strains of avian influenza virus.

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Figure Legends

Figure 1. Major contemporary flyways of migratory birds connecting Southeast Asia with the Americas summarized from (30, 31).

Figure 2.

Extinction (● extinct, ○ extant) as related to reproductive rate (y-axis) log mass (x-axis), and likelihood of exposure to water contaminated by waterfowl feces. **(A)** Low contamination. **(B)** Moderate contamination. **(C)** High Contamination. Diagonal lines show estimated probabilities of extinction, as fit by a logistic regression model. Heavy diagonal line indicates the point at which there is a 50% chance of extinction.

Representative extant and extinct species: **(A)** Northern Flying Squirrel (FS), Noblest Chipmunk (NC), Gray Wolf (GW), Cougar (C), Bighorn Sheep (BH), Mountain Goat (MG), Black Bear (BB), Mountain Deer (MD), Elk (E), Muskox (MO), Bison (B). **(B)** Bog Lemming (BL), Northern Collared Lemming (CL), Pronghorn Antelope (P), Grizzly Bear (GB), Polar Bear (PB), Sabertooth Cat (SC), American Lion (AL). **(C)** California Vole (CV), McNown's Vole (MV), Dire Wolf (DW), American Cheetah (AC), Western Horse (WH).

Significance tests: Full model (log mass, log reproductive rate and level of contamination): $X^2(4) = 208.6$, $p < 0.0001$; Log mass: $z = 3.18$, $p = 0.0007$; Log reproductive rate: $z = -2.19$, $p = 0.0142$; Contamination: $X^2(2) = 25.5$, $p < 0.0001$.

Multiple comparisons for levels of contamination: Low vs. Moderate: $z = 1.76$, $p = 0.0801$; Low vs. High: $z = 4.94$, $p < 0.0001$; Moderate vs. High: $z = 3.32$, $p = 0.0009$.

1 **Supporting Online Material**

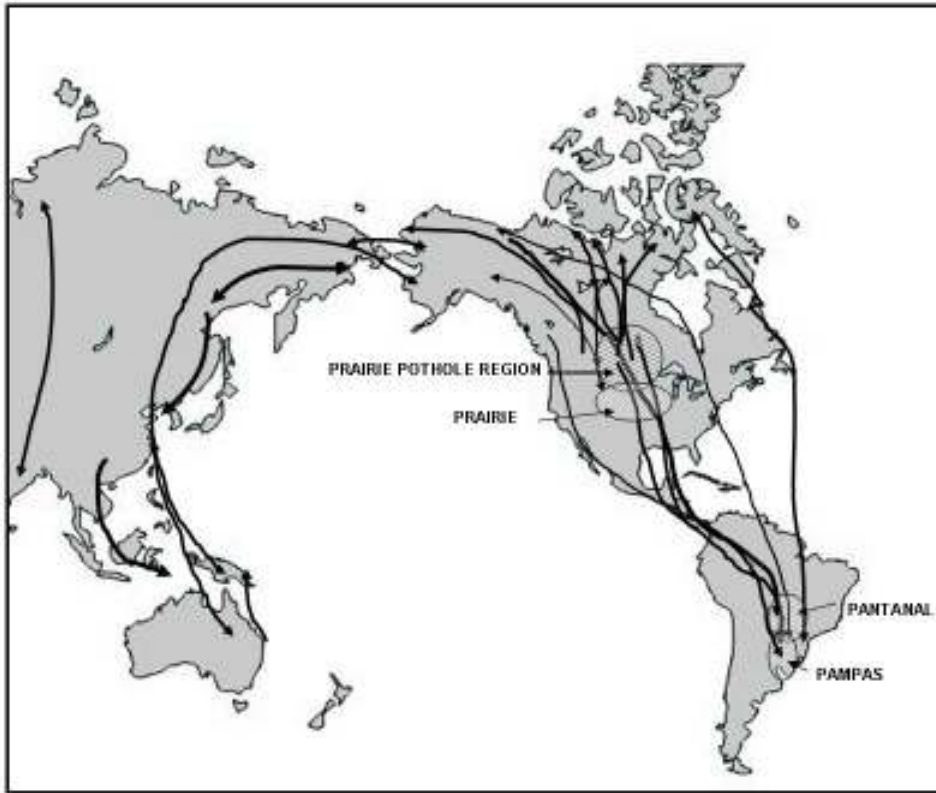
2 **Methods**

3 **Table S1.**

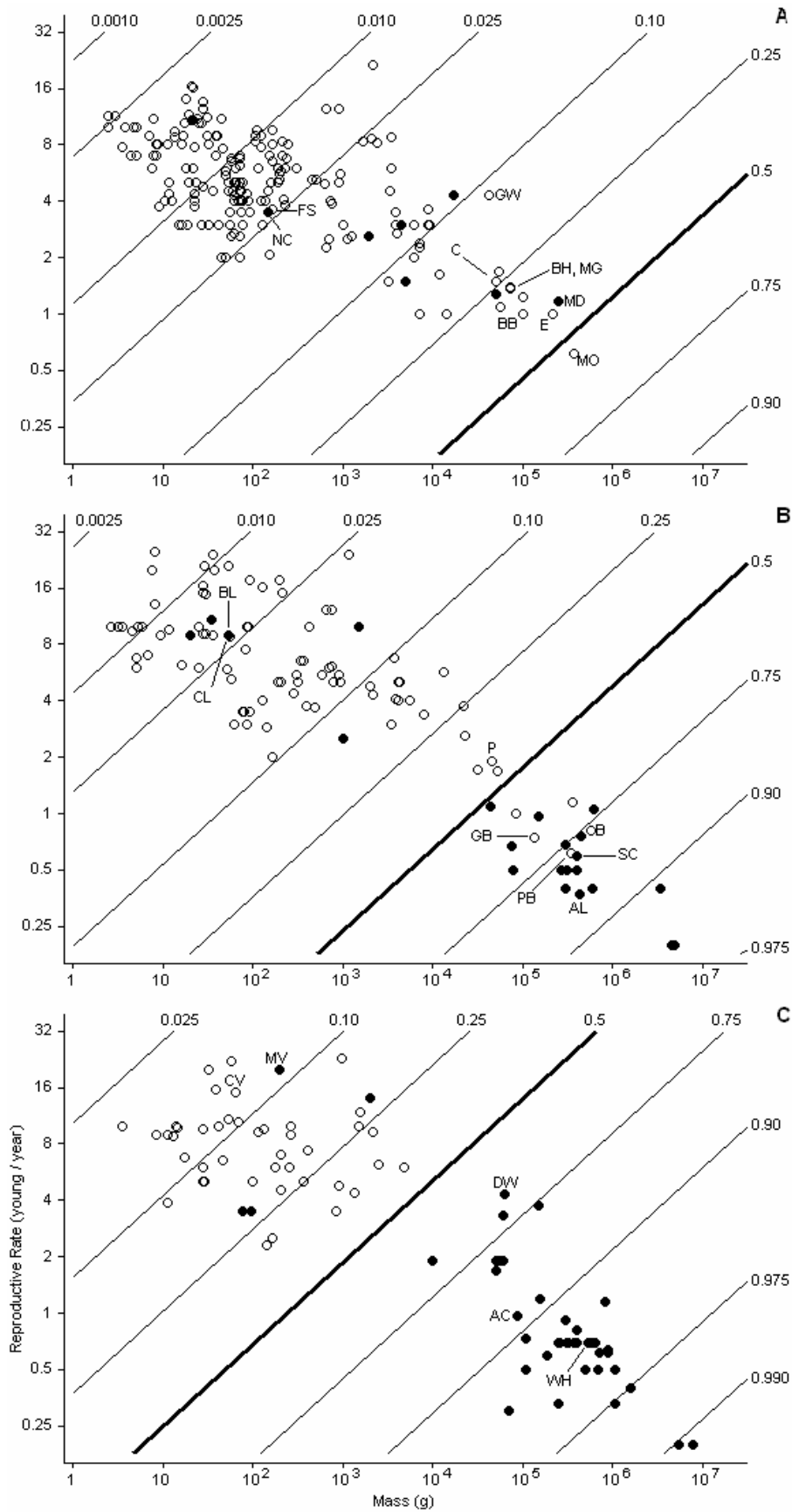
4 **References**

1 **Figures**

2 **Fig. 1.**



3



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Fig. 2.