

Gone forever



Photo/The Bell Museum of Natural History.

A contemporary look at the extinction of the Passenger Pigeon

Was overhunting the cause of the Passenger Pigeon's demise or was the bird an early victim of technology?

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THREE HUNDRED YEARS AGO, THE Passenger Pigeon (*Ectopistes migratorius*) was the world's most abundant land bird. Although found only in eastern North America, it numbered three to five billion, accounting for about a quarter of all North American land birds. Passenger Pigeons traveled in flocks of hundreds of millions, at times obscuring the sun. More than a century has passed since the last gigantic nesting colonies, and over seventy years since the death of the last Passenger Pigeon, Martha, in the Cincinnati Zoo. Although there has been much speculation about the extinction of the Passenger Pigeon since that time, most of the proposed explanations are inadequate.

The Passenger Pigeon was never seriously studied while it still existed and the published accounts are incomplete and often contradictory. Most of our information comes from reports in the scientific and popular literature of the late nineteenth and early twentieth centuries. Little has been written about the Passenger Pigeon's role as an important component of the eastern deciduous forest ecosystem. Its reproductive behavior exploited the mast fruiting of these trees, which in turn supported the tremendous Passenger Pigeon populations. One of the keys to the bird's success lay in its ability to numerically overwhelm its predators.

The precipitous decline of the Passenger Pigeon from 1871 to 1880, and the birds' subsequent extinction, was an inescapable demographic consequence of the relentless disruption of the nesting colonies, which resulted in repeated nesting failures. This was facilitated by the development of the eastern railroad network and the telegraph, which made every colony accessible to market harvesting. Overhunting did not exterminate the Passenger Pigeon, as is commonly believed, rather, over two decades, cohorts died without the opportunity to replace themselves.

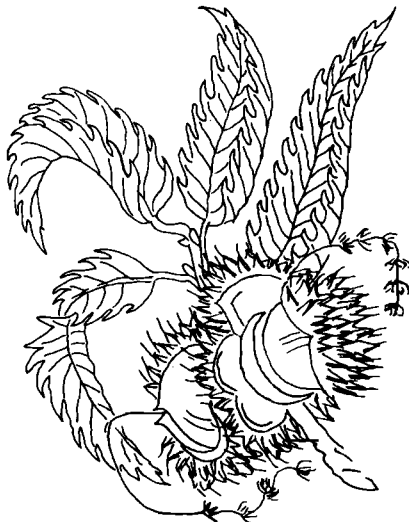
IN ORDER TO UNDERSTAND THE EXTINCTION of the Passenger Pigeon, its ecology and incredible abundance must first be considered. Nomadism and colonial behavior were critical to the Passenger Pigeon's success. The birds nested in colonies containing millions of pairs,



Beech leaves and mast



Oak leaves and mast



Chestnut leaves and mast

Passenger Pigeons often disgorged the contents of their crops in order to consume a more favored food. They preferred beech mast over acorns, and buckwheat more than wheat. Audubon estimated that 1,115,136,000 birds consumed 8,712,000 bushels of mast daily.

traveled together to feed, and roosted together at night. During spring migration and the breeding season, the entire population consisted of an amazingly small number of groups, probably fewer than a dozen. These groups were stupendous, often filling the sky and taking days to pass over an area. The descriptions of these flights—"indescribable multitudes," "so thick that they obscure the light"—would be unbelievable were they not repeated by so many authors. The largest flight ever recorded was estimated to contain 2,230,270,000 birds (Wilson 1832). By traveling and nesting in such large groups each pigeon was essentially shielded from predators, a concept known as predator satiation. Wherever the pigeons went there were not enough local predators to seriously detract from their numbers.

How could so many pigeons find enough food? Before settlement by Europeans, eastern North America was almost completely covered by deciduous forest. Several of the forest trees—beech, oaks, and chestnut—produced large nutritious nuts that were the main food of the Passenger Pigeons. Every few years in any given area, these trees produced enormous crops of nuts. This pattern of "mast fruiting" at unpredictable times enabled the trees to satiate their local seed predators—as colonial behavior enabled the pigeons to satiate their predators—and thus increase their reproductive success. Flocks of Passenger Pigeons roamed the forest, often flying hundreds of miles a day, until they found an area with a heavy mast crop. They remained there until they depleted the food supply. So efficiently did they scour the forests that hogs sometimes starved in their wake. In summer, when nuts weren't available, the Passenger Pigeons wandered to the northern Great Lakes states and Canada to feed on a wide variety of berries. Because the pigeons dispersed after nesting, the summer and fall flocks were smaller in comparison with the spring flights, but still huge. In late fall and winter the flocks continued their nomadic wandering through the southern United States, where acorns were the main food. Here the pigeons formed tremendous roosts, often breaking limbs and destroying trees by their collective weight. Some of these fall and winter roosts were at traditional sites, occupied whenever there was a sufficient food supply.

Nesting colonies formed in the spring where large crops of nuts from the past

autumn remained on the ground. Because the locations of large mast crops changed from year to year, Passenger Pigeons rarely nested in the same place in two consecutive years. After certain poor mast years, there was probably no major nesting attempt. In most years, at least one enormous colony nested in the east (usually in the forests of New York or Pennsylvania) and one in the midwest. During the 1800s, the midwest colony usually nested in Michigan, where it fed on beech mast, and in alternate years, in Wisconsin, where the birds fed on acorns.

A nesting usually consisted of several colonies in adjacent counties. The largest nesting ever recorded carefully, in Wisconsin in 1871, covered 850 square miles and comprised at least 135 million adults (Schorger 1937). Every suitable tree had nests, sometimes fifty or more, each containing only one egg. Nesting within a colony was highly synchronous, with most of the eggs laid on the same day. There were so many nests that nonhuman predators could hardly affect nesting success.

Certain aspects of their biology, shared with other doves and pigeons (Columbiformes), allowed Passenger Pigeons to form these gigantic nesting colonies. Their tremendous mobility, granivorous diet, and the production of pigeon milk* in the crops of breeding adults, allowed the birds to provide their nestlings with food gathered far from the nesting colony. Like other columbids, the parents exchanged nest-tending duties twice daily, with the male on the nest for about six hours at midday and the female on for the remainder of the time. This allowed each parent time to travel far enough to get food for itself and its nestling. The difficulty of providing enough food for two nestlings and pressures to keep the nesting period as short as possible may have been factors working to limit the clutch size to a single egg.

The nesting season usually began in April and concluded in May or June. This only allowed time for one or two nestings a year, but there is no evidence that any individual attempted a second brood after a successful nesting. It is known that pairs replaced clutches, especially those destroyed by late snowstorms. The nesting season seems to have been controlled by the availability of nuts; the supply

*a curd-like substance produced by both sexes at hatching time to feed the young. Though it contains no sugar, it resembles mammalian milk in that it consists of salts, fats and proteins.



Passenger Pigeon.
COLUMBA MIGRATORIA, Linn
Male, 1. Female, 2.

Drawn from Nature & Published by John J. Audubon, F.R.S. &c.

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diminished rapidly each spring as a result of germination and consumption not only by pigeons, but also by insects, microorganisms, mammals, and other birds. Although Passenger Pigeons ate a variety of fruits and seeds, the mast crops were essential for nesting.

The local impact of a Passenger Pigeon flock was devastating. Schultz (*in* McKinley 1960) describes a roosting area in Missouri where a forty acre area "had the appearance of having suffered from a hurricane or tornado." A great deal of timber was destroyed at these roost sites. Dung accumulated beneath the roost trees to a thickness of several inches or more, killing the vegetation, although ultimately enriching the soil. Passenger Pigeons may have been important dispersal agents of forest trees, transporting undigested seeds in their crops (Webb ms.).

The effects of a flock of Passenger Pigeons on the local fauna was equally impressive. Nut-eating animals such as squirrels, chipmunks, and Blue Jays faced severe local competition from Passenger Pigeons. Raptors and mammalian predators took full advantage of a pigeon colony. In reference to a roost in Kentucky, Audubon (1831:323) wrote, "The howlings of the wolves now reached our ears, and the foxes, lynxes, cougars, bears, raccoons, opossums, and pole-cats were seen sneaking off, whilst eagles and hawks of different species, accompanied by a crowd of vultures, came to supplant

them and enjoy their share of the spoil."

BY ALL ACCOUNTS, THE FINAL decline of the Passenger Pigeon was rapid. It is impossible to know whether population levels in the mid-1800s were comparable with those under primitive conditions. Pigeon numbers declined first in the East, perhaps as early as the late eighteenth century (Schorger 1955), then in the Midwest. Several writers have suggested that this was owing to deforestation for human agriculture.

There were still hundreds of millions of Passenger Pigeons left in the early 1870s, when they were still regarded as pests by Michigan farmers (Barrows 1912:246). The 1870s was a decade of catastrophic decline but the nesting population in 1878 was still conservatively estimated at 50 million (Fischer 1913). The Passenger Pigeon became scarce in the 1880s and was very rare in the 1890s. The last reliable specimens were of single individuals collected in Wisconsin in September 1899 (Schorger 1938) and Ohio in March 1900 (Henniger 1902). The last authentic sight record has been much debated. A two year reward campaign, sponsored by the American Ornithologists' Union from 1910-1911 to determine whether the Passenger Pigeon was extinct, failed to discover any convincing evidence of its existence (Hodge 1911, 1912).

The causes of extinction have been the

subject of great speculation: unknown diseases, "loss of vigor," mass drownings, emigration to South America or Australia. Yet, at the time, some ornithologists understood quite well "that all other theories . . . to account for the destruction of the birds by other causes than man's agency are absolutely inadequate" (Forbush 1913). The most obvious human impact on pigeons was the direct killing of adults and young. This was accompanied by habitat destruction through deforestation that might, in time, have been fatal to the species. However, neither overharvesting nor habitat destruction by themselves are sufficient causes for the extinction of the Passenger Pigeon.

Although deforestation probably affected the Passenger Pigeons' decline in the East, adequate forest areas still existed at the same time the bird was becoming scarce. In the major nesting area of north-central Pennsylvania, deforestation began in 1872 but did not reach full speed until 1892 (French 1919:110). Deforestation came even later to Ontario (Mitchell 1911). Michigan was still well wooded in 1883, although being logged rapidly (Rand McNally and Co. 1883). Logging was initially concentrated on pines, which were much less important to Passenger Pigeons than deciduous trees.

The Passenger Pigeon was exterminated because pigeon harvesting activities by humans prevented recruitment to the



Methods of collecting pigeons varied: young were knocked from nests with long poles; nesting trees were cut down or set on fire; birds were suffocated by burning sulphur under nesting trees; netting and the use of "stool pigeons" were most commonly used. The Bettmann Archive.

population; entire cohorts died without replacing themselves. Forbush (1913) stated a similar opinion: "The destruction of most of the young birds for a series of years would bring about such a diminution of the species as occurred soon after 1878." How did this happen?

THE ARRIVAL OF FLOCKS OF PASSENGER Pigeons always meant food to the local people, whether natives or settlers. Nevertheless, people probably had little impact on the number of pigeons until they began harvesting them for market instead of for the home only. Market harvesting began before 1800, but was not a major industry until 1840.

Two technological developments of the 19th century increased the efficiency and scope of market harvesting to the point where it was ultimately responsible for the extinction of the Passenger Pigeon. The seemingly unrelated advances were those of the railroad and the telegraph.

In 1830, there were only 23 miles of railroad track in the United States (Rand McNally and Co. 1883). By the time of the Civil War, there were over 30,000 miles of track and a railroad network through most of America east of the Mississippi River was complete (Chandler 1965). This network allowed the professional pigeoners, who numbered about 1000 in their heyday, rapid access to all major nesting colonies. Equally important, it provided a quick way to ship barrels of pigeons to the big city markets in the east and midwest. In 1800, travel between New York and Chicago took six weeks. By 1830, it took only three weeks, and by 1857 it took less than two



Known for its maneuverability and speed and grace in flight, the Passenger Pigeon's well-deserved nickname was the "blue meteor." Photo/The Bell Museum of Natural History.

days. Freight moved almost as fast, taking, in 1849, nine transfers and nine days to go from Philadelphia to Chicago. By 1859 this took three days without transfer (Chandler 1977).

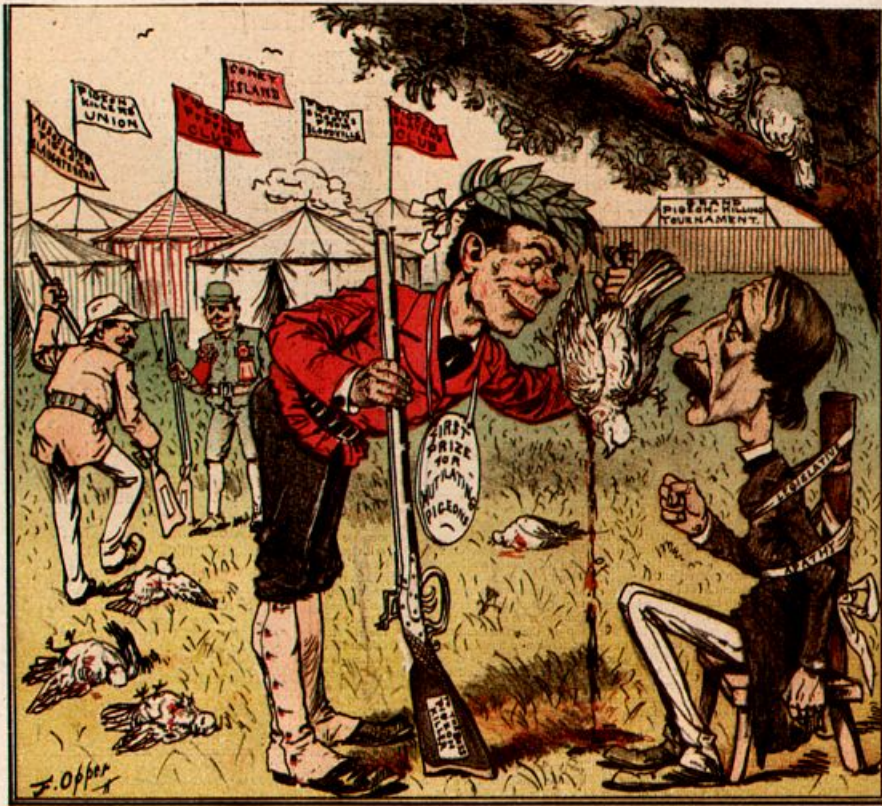
The telegraph served to keep the professional pigeoners informed of the locations of nesting colonies. The entire operation was efficiently, although informally, organized so that word of any nesting of pigeons spread rapidly for hundreds of miles. The railroad companies benefitted from the pigeon harvest and transport, so they undoubtedly helped in seeing that this information was transmitted.

After 1861, only a handful of colonies were too far from rail or ship for market exploitation. In 1881, even a nesting colony in Oklahoma that was 110 miles from the nearest railroad was plundered by professionals who used teams and wagons to haul out their quarry.

The impact of the harvest was staggering. At the 1860 nesting near Grand Rapids, Michigan, pigeoners shipped 588 barrels—over 100,000 pounds—of pigeons to market. At 350 pigeons per barrel, more than 200,000 pigeons went to distant markets from that nest site. Including local markets and home use, birds that died in the nest, and birds left



The development of a nationwide railway system made it possible to get the birds quickly to market. Five thousand barrels were shipped from a single nesting (30 dozen birds to the barrel), at a cost per barrel of \$6 to \$12. The telegraph kept hunters informed of nesting locations.



An early environmental lampoon from the late 19th century. Protests against the mass slaughter of Passenger Pigeons began as early as 1875, mostly against trap shooting. Laws were passed in the early 1880s prohibiting shooting at the nesting sites, but they were ineffective. The Bettmann Archive.

for the hogs to clean up, probably as many as one million birds were destroyed at this single nesting. Harvests of this magnitude continued for another 20 years! The largest harvest was probably at Petosky, Michigan, in 1878, where the nesting colony covered nearly 250 square miles. In three months, 1.5 million dead and more than 80,000 live birds were shipped by rail, and probably as many by water. Up to 10 million pigeons may have perished at that nesting alone.

THREE MAIN METHODS WERE USED TO capture Passenger Pigeons: netting adults, shooting adults, and taking the young from the nest.

Most professional harvesters captured adults in nets at baited sites near the nesting grounds. A single release of the net often took more than 100 birds. Although this technique was used since the 1600s or earlier and millions of pigeons were killed this way, netting alone could not

have wiped out the species because the rest of the pigeons in the colony continued to nest, apparently undisturbed by the netting activities.

Although market harvesters probably accounted for most of the mortality, every nesting colony was invaded by shot-gunners, many of whom were locals, but also included well-heeled sportsmen from distant cities, whose harassment of the nesting birds was intense. People shot birds within the nesting colony, even at the nest. The commotion probably caused individuals and even whole colonies to abandon their nests.

The fat nestlings were prized even more than the adults. Professionals and locals alike used every conceivable method to harvest the nestlings—chopping down the nest trees, knocking the young out of the nest with poles, and even setting the nest trees on fire to cause the adults and young to jump out. In a typical densely populated colony it was possible to harvest nearly all the young.

Despite the scale of the slaughter, overhunting did not exterminate the Passenger Pigeon, as it nearly had the bison.

Instead, Passenger Pigeons became extinct because over a period of about 20 years—twice an individual's lifetime—adults were prevented from replacing themselves, directly by the nestling harvest and indirectly by the shooting, which led to nest abandonment. Had reproduction continued, it is unlikely that netters and shooters away from the nesting sites could have exterminated the Passenger Pigeons. There were simply too many pigeons for the harvest of adults to be complete.

The first record of a nesting colony being abandoned because of shooting was in 1869 in Wisconsin. Laws passed in the early 1880s to prohibit shooting near the colonies were ineffective; abandonment by adult birds became even more common.

Slaughter at the nesting colonies continued to the end. The last known attempt at colonial nesting was in 1887, in Wisconsin. These birds left about two weeks after they started to nest, probably disturbed by shooting.

What happened once the Passenger Pigeon population was reduced to a small number of old birds? Was extinction inevitable, or could the population have persisted at low levels? Halliday (1980) and others have argued that the social facilitation of a large colony was necessary for the Passenger Pigeons to breed, so that once the population fell below a critical size there was no attempt at reproduction. However, it is well documented that some Passenger Pigeons, albeit a small number, nested solitarily and in small groups even when the species was superabundant. Some pairs bred successfully in captivity (Deane 1881, 1896).

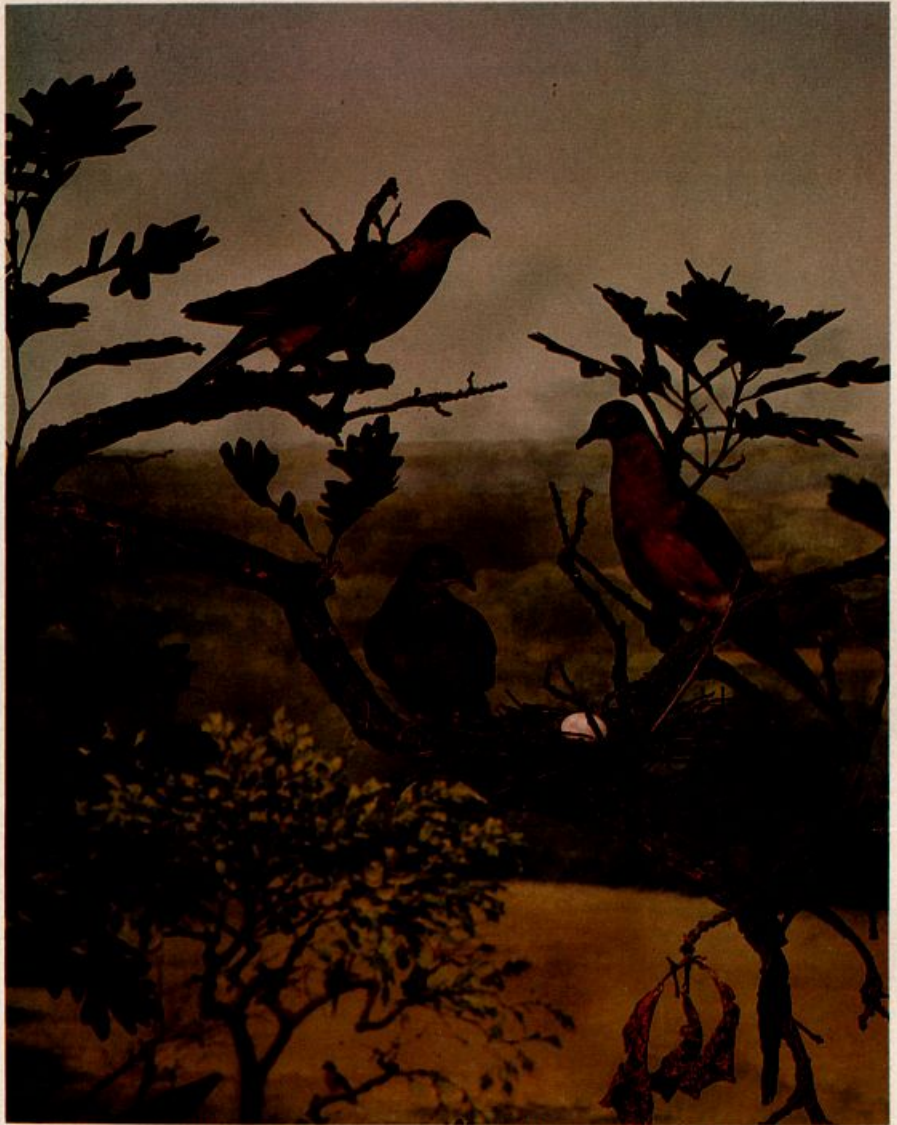
The pigeons continued to attempt to breed even after the population was reduced to low levels. Some reproductive success occurred; many of the last specimens taken were young birds. Nest success in these last small colonies and by the lone pairs must have been pitifully low. Without the numerical protection provided by the large colonies, the birds were unable to satiate the local predators. These last birds were doomed as they attempted solitary nesting, building unconcealed nests, and laying only a single white egg. This very low rate of reproduction was just not enough to save the species, whose whole reproductive strategy depended on mass nesting. And so, the Passenger Pigeon, which was once the most abundant land bird on the planet, vanished forever.

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The nest and egg of the Passenger Pigeon. Once the number of birds was reduced to a few, its uncamouflaged nests and solitary white egg jeopardized its survival. Photo/The Bell Museum of Natural History.

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