

Drastic population fluctuations explain the rapid extinction of the passenger pigeon

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To assess the role of human disturbances in species' extinction requires an understanding of the species population history before human impact. The passenger pigeon was once the most abundant bird in the world, with a population size estimated at 3–5 billion in the 1800s; its abrupt extinction in 1914 raises the question of how such an abundant bird could have been driven to extinction in mere decades. Although human exploitation is often blamed, the role of natural population dynamics in the passenger pigeon's extinction remains unexplored. Applying high-throughput sequencing technologies to obtain sequences from most of the genome, we calculated that the passenger pigeon's effective population size throughout the last million years was persistently about 1/10,000 of the 1800's estimated number of individuals, a ratio 1,000-times lower than typically found. This result suggests that the passenger pigeon was not always super abundant but experienced dramatic population fluctuations, resembling those of an "outbreak" species. Ecological niche models supported inference of drastic changes in the extent of its breeding range over the last glacial–interglacial cycle. An estimate of acorn-based carrying capacity during the past 21,000 y showed great year-to-year variations. Based on our results, we hypothesize that ecological conditions that dramatically reduced population size under natural conditions could have interacted with human exploitation in causing the passenger pigeon's rapid demise. Our study illustrates that even species as abundant as the passenger pigeon can be vulnerable to human threats if they are subject to dramatic population fluctuations, and provides a new perspective on the greatest human-caused extinction in recorded history.

genome sequences | ancient DNA | toe pad

Rare species with restricted geographic distributions are more likely to go extinct than abundant, widespread species because the former are more vulnerable to environmental stochasticity, diseases, and human disturbances (1). Therefore, the extinction risk of common species tends to be ignored. As a result, factors responsible for the extinction of once abundant species, whose demise could impact ecosystems profoundly, are not well understood. A species with dramatic population cycles could be especially vulnerable to extinction when it becomes rare (2, 3), and large-scale population fluctuations could increase extinction risk (4). Hence, knowledge of long-term demographic history allows a better perspective on a species' extinction risk than a snapshot of population size (4, 5).

Applying population genetic analysis to ancient DNA (aDNA) extracted from the remains of extinct species can improve our understanding of the species' history and potential reasons for its extinction (6). Estimating extinct species' demographic history is, however, often difficult because specimens are scarce and the quality of remaining DNA is poor (7). By adapting high-throughput sequencing technologies, we obtained high-quality genome sequences for the passenger pigeon (*Ectopistes migratorius*), which

went extinct 100 y ago. These sequences allowed us to estimate the long-term population history in unprecedented detail and to provide a novel hypothesis as to why the most abundant bird the world had known became extinct so rapidly.

Migratory flocks of the passenger pigeon were once so immense that they were said to have blanketed the skies of eastern North America (8). In one of many illustrative descriptions, John James Audubon recounted a mile-wide flock of migrating passenger pigeons that passed overhead, blocking the sun for 3 consecutive days (9). The vast numbers of passenger pigeons have led ecologists to suggest that this bird was a keystone species in North American ecosystems (10, 11). This pigeon is believed to have influenced forest composition by consuming and dispersing acorns, beechnuts, and other mast crops on which it fed (10, 11), disrupted local communities, out-competed other mast-eating species, damaged trees by the weight of large flocks leading to breaking of large limbs of trees, and killed surface vegetation with thick layers of excrement (8, 11).

Although the passenger pigeon population was estimated at 3–5 billion individuals in the early and middle 1800s, the last passenger pigeon died at the Cincinnati Zoo on September 1, 1914 (8). The extinction of this abundant bird in a mere five decades is a poignant reminder that even a bird numbering in

Significance

The number of passenger pigeons went from billions to zero in mere decades, in contrast to conventional wisdom that enormous population size provides a buffer against extinction. Our understanding of the passenger pigeon's extinction, however, has been limited by a lack of knowledge of its long-term population history. Here we use both genomic and ecological analyses to show that the passenger pigeon was not always super abundant, but experienced dramatic population fluctuations, which could increase its vulnerability to human exploitation. Our study demonstrates that high-throughput-based ancient DNA analyses combined with ecological niche modeling can provide evidence allowing us to assess factors that led to the surprisingly rapid demise of the passenger pigeon.

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the billions can be driven to extinction within a human lifetime (8, 12, 13). The passenger pigeon is thought to have depended on large flocks for predator satiation and efficient location of unpredictable seed mast crops (12, 13), and a minimum population-size threshold was required for successful breeding (14). Whereas human involvement in its extinction has been commonly assumed (8, 14), the magnitude and potential significance of natural fluctuations in its population remain unexplored. If the passenger pigeon population had repeatedly and dramatically risen and fallen, and human disturbances overlapped with a decline phase, anthropogenic factors could have prevented it from recovering from a population minimum, leading to its rapid extinction. In this study, we used aDNA genomic analyses, ecological niche modeling, and reconstructions of the acorn base on which it fed to show that the passenger pigeon experienced recurring population fluctuations of large magnitude.

Results and Discussion

To estimate effective population size, we extracted aDNA from toe pad tissues of four museum specimens collected across the breeding range (*SI Appendix, Fig. S1*). Three of the four specimens yielded usable genome sequences for population genetic and demographic analyses (Table 1). We obtained genome sequences of 0.74–0.99 Gb with 5- to 20-fold average coverage (Table 1 and *SI Appendix, Figs. S2–S4 and Table S1–S3*) by mapping sequence reads generated against the draft genome (1.09 Gb) of a domestic pigeon (*Columba livia*) (15). That is, we obtained between 68% and 91% of the maximum sequence length by mapping against this reference genome and recovered 57–75% of each passenger pigeon's genome, assuming that the sizes of the two pigeon species' complete genomes were similar (1.3 Gb) (15). To our knowledge, this is the longest genome sequence with the highest quality ever obtained for an extinct avian species.

The mean nucleotide difference (d_{xy}) between the genomes of the passenger pigeon and the domestic pigeon was 0.028. The genetic distance between the genomes of two passenger pigeons from the western part of their breeding range ($d_{xy} = 0.0036$) was similar to those between either of them and one from the eastern part ($d_{xy} = 0.0034$ and 0.0039), suggesting no population structure in this species. This inference fits with the conventional knowledge that flocks of passenger pigeons moved to different areas for breeding every year (8). The genetic diversity of the passenger pigeon genomes [$\pi = 0.0027 \pm 0.0015$ (SD)] is consistent with those of other avian genomes (0.0007–0.0036) (*SI Appendix, Table S4*).

We used two approaches to estimate genetically effective population size (N_e). We first used the Generalized Phylogenetic Coalescent Sampler (G-PhoCS) (16) based on the three passenger pigeon genomes combined, yielding a long-term average genetically effective population size (N_e) of 3.3×10^5 (95% credible interval = $3.25\text{--}3.32 \times 10^5$) (Fig. 1 and *SI Appendix, Fig. S5*). Then, we used the pairwise sequentially Markovian coalescent (PSMC) (17) analyses based on the three genomes individually to estimate N_e change through time. The PSMC estimates were the same order-of-magnitude as the G-PhoCS estimate, and showed N_e fluctuating between 0.5 and 1.7×10^5 over the last million years, decreasing significantly from the last interglacial period (LIG, approximately $1.1\text{--}1.3 \times 10^5$ y before present) to a minimum at the last glacial maximum (LGM, approximately 2.1×10^4 y before present) and then recovering (Fig. 2 and *SI Appendix, Figs. S6 and S7*). The three genomes returned concordant PSMC population trajectories, suggesting no population structure in this species (18), consistent with the genetic distance analyses.

Unexpectedly Small Effective Population Size. The passenger pigeon's N_e is not larger than those of other regionally or continentally widespread birds ($N_e = 1.3 \times 10^5 - 2.4 \times 10^7$) (*SI Appendix, Table S5*). It is also much lower than expected given the census population size (N_c) of 3–5 billion. N_e is on average one-tenth of N_c (19), and the value of ~ 0.0001 for N_e/N_c inferred in this study is much smaller than those estimated from other animals' genome sequences ($0.0125 - \sim 1$) (*SI Appendix, Table S6*) or from nongenomic data on other birds ($0.05\text{--}0.74$) (19).

N_e is sensitive to population fluctuations (20, 21); in particular, low values of N_e occurring at population minima anchor N_e so that the extremely low N_e/N_c suggests remarkably large population fluctuations (19, 21, 22). A low N_e/N_c is typical of outbreak species, which are characterized by dramatic and recurrent changes in population size (21, 23). For example, the Australian plague locust (*Chortoicetes terminifera*) can reach as many as 100 billion individuals during outbreak phases, yet its estimated N_e is merely approximately half a million (24). If the population of passenger pigeons behaved in a similar way, only occasionally numbering in the billions during "outbreak" phases, we would expect a low N_e for this bird over the last million years, which we found in this study. A low N_e would also have been observed if the passenger pigeon population had remained small until a recent population explosion, as in the case of humans (current

Table 1. Genome mapping information summary for the four passenger pigeon samples

Variable	Museum no.			
	BMNH794	BMNH1149	BMNH3993	AMNH753720
Sex	Male	Male	Male	Female
Locality	Minneapolis, MN	Grand Marais, MN	Marple, PA	English Lake, IN
Tissue size (mm)	5×2×2	5×2×2	5×2×2	2×1×1
DNA volume (ng)	340	822	398	~0
Insert size (bp)	209	159	99	116
Number of reads	1,288,289,698	1,196,720,052	2,086,602,005	1,097,254,178
Number of bases (Gb)	115.94	107.70	187.79	98.75
Mapped rate (%)	41.05	35.99	22.50	11.60
Duplication rate (%)	50.33	56.06	50.35	38.43
Average coverage	19.91	12.98	17.69	5.45
Mapped length (Gb)	0.992	0.972	0.738	0.761

"Insert size" indicates the length of the Illumina genomic sequencing library. "Mapped rate" indicates the percentage of reads mapped to the domestic pigeon genome (National Center for Biotechnology Information accession no. AKCR00000000) using Burrows–Wheeler Aligner (48). "Average coverage" indicates the average value of sequencing depth over all mapped sites. "Mapped length" indicates the length of genome that was mapped by the Illumina reads.

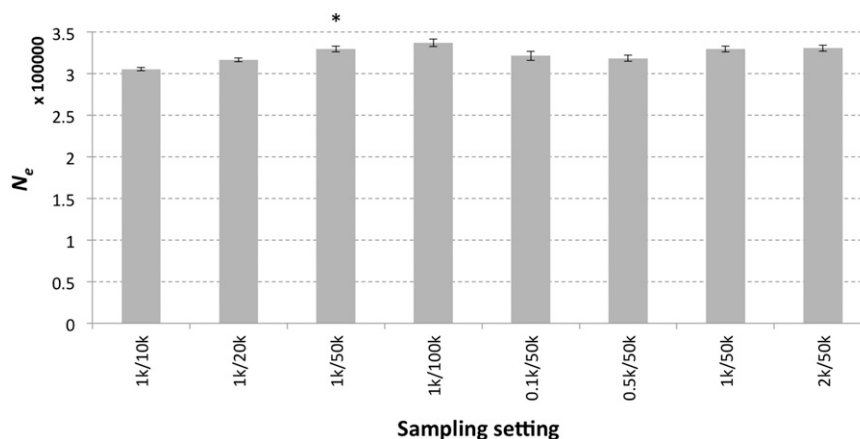


Fig. 1. Long-term average effective population size (N_e) estimates of the passenger pigeon. N_e estimates were constructed using G-PhoCS based on different locus sampling settings. Each histogram and bar describes the mean value and 95% credible interval of N_e based on a certain model and dataset. The sampling settings include 1-kbp loci separated from each other by 10, 20, 50, and 100 kbp, indicated by 1k/10k, 1k/20k, 1k/50k, and 1k/100k, respectively, and 0.1-, 0.2-, 1-, and 2-kbp loci separated from each other by 50 kbp, indicated by 0.1k/50k, 0.5k/50k, 1k/50k and 2k/50k, respectively (see *SI Appendix* for details). The N_e based on the sampling setting of 1k/50k (indicated by an asterisk) is reported in the main text.

human N_c is 7×10^9 and long-term N_e ranges around $0.9\text{--}1.7 \times 10^4$ (16, 17, 25), but our ecological analyses support a history with repeated rises and falls in population size (see below).

Environmental Conditions in the Past Support Large Population Fluctuations. Because population size depends on environmental suitability (26), we constructed ecological niche models (ENMs) to assess whether changes in the pigeon's breeding range between the LIG, LGM, and current day would provide independent support for large fluctuations in population size. By associating current species occurrences with environmental conditions, ENMs can reveal species' ecological niches in environmental space, which are then mapped to a geographic area to reveal their potential distributions (27, 28). Our purpose here is to estimate the potential magnitude of population fluctuations in potential areas suitable for breeding passenger pigeons.

The ENMs using a threshold that allows for a maximum of 1% omission rate indicated that areas with suitable climatic conditions for breeding passenger pigeons were much more limited at the LGM than at the LIG (47-times LGM) and at present

(60-times LGM area) (Fig. 3). The mobility-oriented parity method (29) identified the areas with novel environments during the LGM (projection region) relative to current day (calibration region), which are concentrated in the northeast and southeast portions of the study area (*SI Appendix*, Fig. S8). However, even if these novel environments caused the ENMs based on the current environmental niche to underestimate the LGM range, our conclusion of a substantial reduction in the LGM ranges is still robust. This result is because the northeast portion of the study area—where model extrapolation issue is most severe—was covered by ice sheets during the LGM (*SI Appendix*, Fig. S9), and thus was not suitable for breeding passenger pigeons. It is, however, unknown how many passenger pigeons could have bred successfully at the LGM in the limited suitable range.

We supported this climate-based analysis of long-term population fluctuations for the passenger pigeon with one based on the post-LGM distribution of oaks inferred from fossil pollen records, current-day median annual acorn production per square kilometer, and estimated daily consumption of acorns by a passenger pigeon, an approach that also allowed us to test the

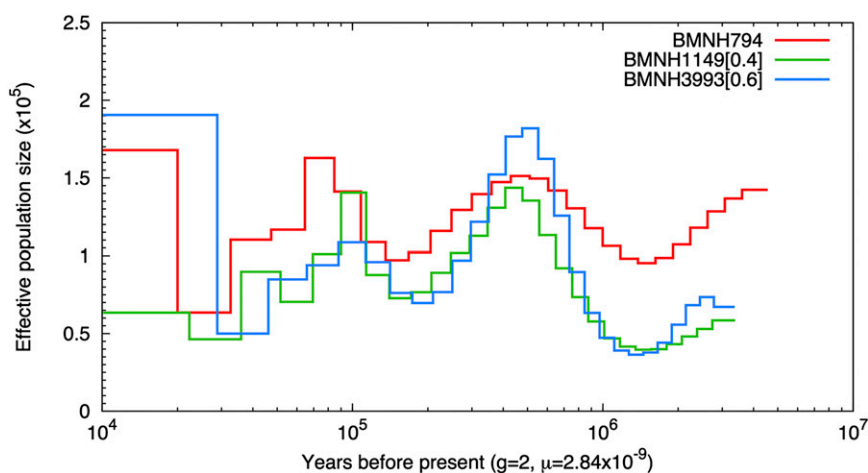


Fig. 2. Demographic history of passenger pigeons. PSMC analyses were applied to individual diploid genomes of three passenger pigeons, BMNH794, BMNH1149, and BMNH3993. Uniform false-negative rate correction was applied to BMNH1149 and BMNH3993 with correction rates of 40% and 60%, indicated by "BMNH1149 [0.4]" and "BMNH3993 [0.6]", respectively (*Methods* and *SI Appendix*). "g" indicates generation time in years, and "μ" indicates genomic substitution rate.

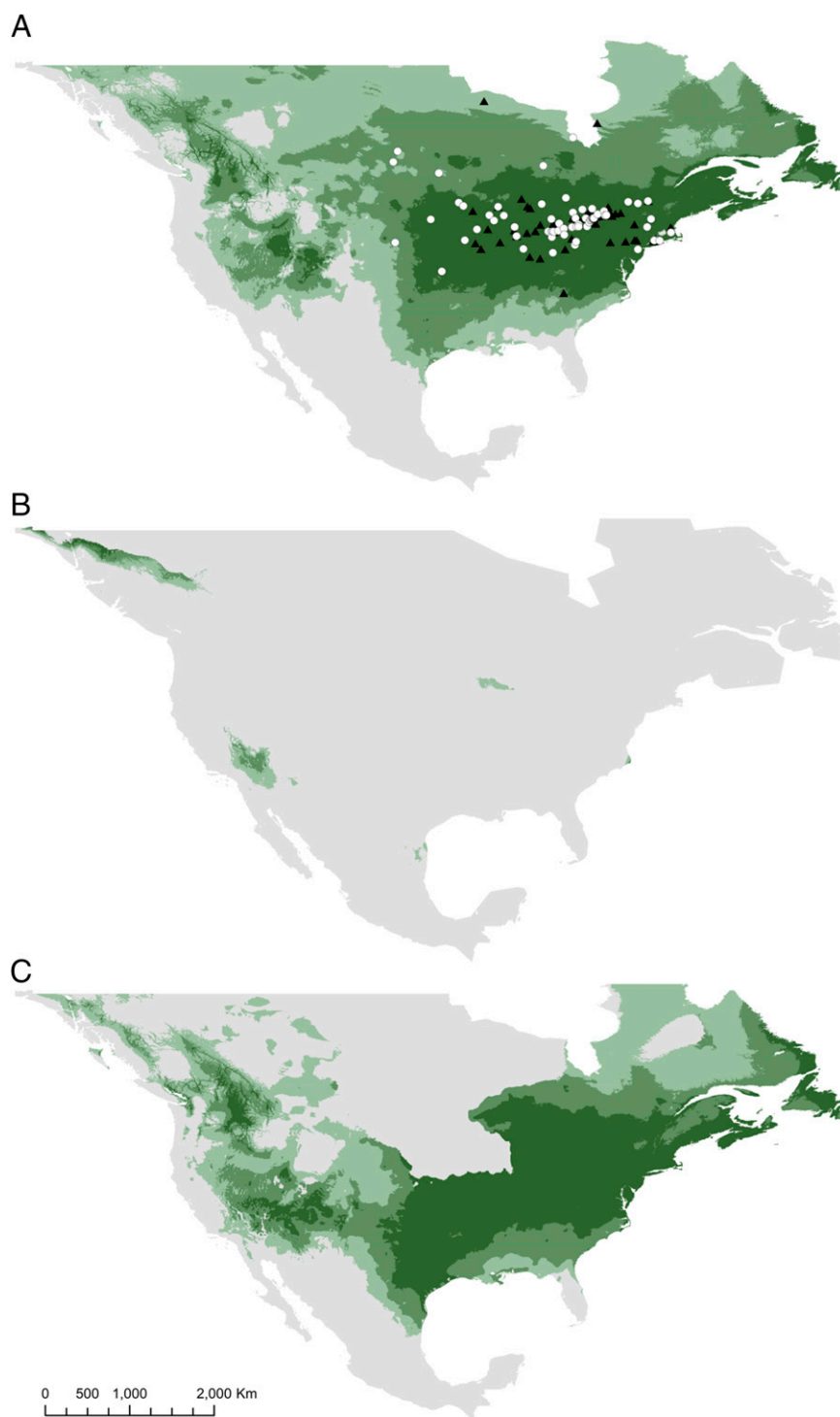


Fig. 3. Predicted breeding ranges of the passenger pigeon. Predicted breeding ranges at current day (A), the LGM (B), and the LIG (C). Predicted breeding ranges are based on ENMs built with 19th century occurrences of breeding passenger pigeons (triangles in A as training data and circles as testing data) and the seven bioclimatic variables that each contributed at least 5% to the current-day model. The green areas delineate potential breeding ranges for the passenger pigeon. Increasing shades of green represent suitable areas for the passenger pigeon using thresholds of increasingly higher omission rates (0%, 1%, and 5%).

accuracy of the early naturalists' N_c estimates. The expansion of oaks from their LGM refugia (*SI Appendix, Fig. S9*) drove an increase in passenger pigeon carrying capacity, which peaked at $1.7\text{--}2.3 \times 10^9$ individuals at 9,000–10,000 y before present, and subsequently stabilized at approximately $1.1\text{--}1.6 \times 10^9$ individuals from 6,000 y before present to present (Fig. 4).

Short-Term Fluctuations in Food Supply. Acorn production varies significantly from year to year across oak species (30, 31). For example, acorn production by red oaks can vary as much as 12-fold between years, and for white oaks as much as 136-fold (*SI Appendix, Table S7*). Inclement weather can cause mast failures over large areas (32) and, as a result, a reduction in population

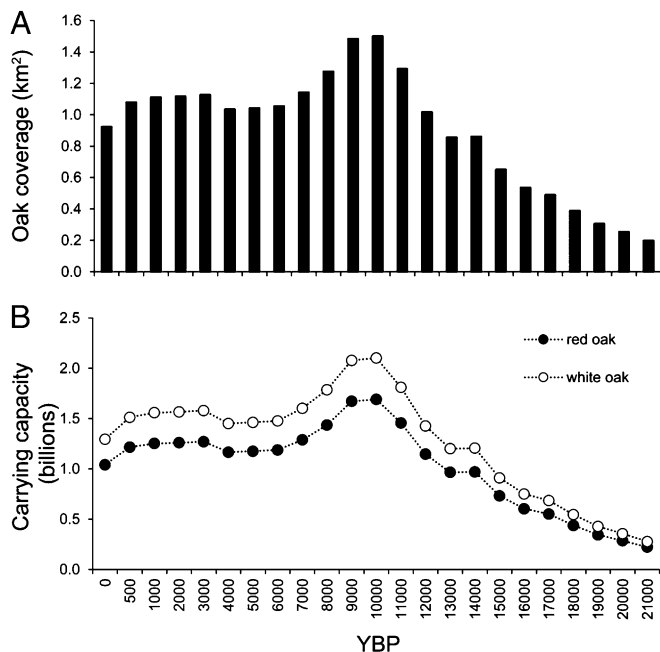


Fig. 4. Historical oak coverage and passenger pigeon carrying capacity from 21,000 y before present (YBP) to present day. (A) Historical oak coverage was converted from fossil-pollen records for northern and eastern North America (SI Appendix, Fig. S11) (47). (B) The carrying capacities of passenger pigeons are annual pigeon abundances that could be sustained by acorn production. The median acorn production of red oaks (*Quercus rubra*, ●) and white oaks (*Quercus alba*, ○) collected from multiple sites and years (SI Appendix, Table S8) (30, 31) were used to calculate carrying capacity.

sizes of mast-consuming species (33–35). Applying similar good-to bad-year variations to the median value calculated above, the projected acorn production could have supported between $0.6\text{--}1.7 \times 10^8$ and $6.7\text{--}8.0 \times 10^9$ passenger pigeon individuals from 6,000 y before present to the present (SI Appendix, Fig. S10), a range for which the peak is consistent with the early naturalists' N_c estimates, but which also shows how large the short-term natural fluctuations might have been.

The ENMs, fossil pollen records, and acorn-production data suggest that the passenger pigeon experienced large, natural population fluctuations, but these do not explain completely the three orders-of-magnitude difference between the estimated and expected N_c inferred from our genomic analysis. Other factors, however, might have also contributed to fluctuations in passenger pigeon's population size, either by reducing past population minima or by increasing the 19th century population.

For example, the pigeon's enormous roosting and breeding colonies might have increased the species' vulnerability to density-dependent regulation resulting from physical damage to trees or outbreaks of infectious diseases (13, 36, 37). Furthermore, the bird's dependence on large flocks (12, 13) could have exacerbated its vulnerability to predation following years of inadequate food supply, thereby reducing population minima further (2). It has also been argued that European immigrants contributed to an outbreak in the numbers of passenger pigeons by providing them with supplementary food resources (e.g., agricultural crops) or releasing them from competition (for mast) and hunting pressures from Native Americans (38, 39).

Conclusions

To our knowledge, our study provides the first empirical perspective on the passenger pigeon's population history. Proper evaluation of factors determining a species' extinction requires

more than the average or a snapshot of its population size. Based on our estimates that the passenger pigeon's N_c was persistent at approximately 10^5 throughout the last million years (Fig. 2), this species probably experienced frequent and dramatic population fluctuations following climatic, food-resource, and other ecological variations, thereby increasing its extinction risk (40, 41). We suggest that before human settlement the passenger pigeon routinely recovered from population lows. We hypothesize that a downward trend in its population size occurred simultaneously with human exploitation in the late 1800s and that the combination of the two triggered its rapid extinction. Once below a minimum threshold population size, the conspicuous roosting and breeding behaviors of this bird could prevent its recovery. This hypothesis may also explain the mysterious extinction of the Rocky Mountain grasshopper (*Melanoplus spretus*), which periodically formed immense swarms and was the most serious agricultural pest in the western North America but went extinct rapidly from the late 1800s to the early 1900s (42). Insights gained from the demise of the passenger pigeon shed light on the vulnerability of abundant species, especially those that are prone to dramatic population fluctuations.

Methods

Genome Sequencing. Genomic sequences were generated applying the Illumina sequencing technology to aDNA extracted from toe pads of four passenger pigeons. Sequences of 90-bp paired-end reads were mapped to the draft genome of a domestic pigeon (15). We performed base quality recalibration, added several quality filters, and excluded Z-linked and mitochondrial genomes for the samples used for genetic diversity estimation and demographic analyses.

Demographic Analyses. We used the G-PhoCS (16) to estimate the long-term average N_e of the passenger pigeon based on three DNA samples with better sequencing qualities by modeling (i) the divergence between eastern and western passenger pigeon populations and (ii) the divergence between passenger pigeons and domestic pigeons. The PSMC (17) were applied to the same three samples to infer the N_e change of the passenger pigeon through time. We performed uniform false-negative rate correction to the PSMC results of the samples with coverage lower than 20.

Breeding Ranges with ENM. We collected 136 19th century occurrences of passenger pigeons in the breeding season to construct their ENMs at current day, LGM, and LIG using Maxent (43). We prepared two lower-dimension datasets based on the 19 bioclimatic variables from WorldClim (www.worldclim.org) as the environmental layers. The first dataset ("high-contribution" dataset) includes seven bioclimatic variables that each contributed 5% or more to current-day model (44). The second dataset ("low-correlation" dataset) includes eight bioclimatic variables that are not highly correlated with one another ($r < 0.8$; ENMTools) (45). We estimated passenger pigeons' breeding ranges using a threshold that allows a maximum of 0%, 1%, or 5% omission rate (46). We performed partial receiver operating characteristic (ROC) analyses (46) to confirm that the ENMs outperformed the random model. We used the mobility-oriented parity method (29) to assess environmental similarity based on multivariate distances (Mahalanobis distances) between current day (calibration region) and LGM or LIG (projection region) to identify geographic areas with high risk of extrapolation biases. The predicted breeding ranges, partial ROC results, and environmental similarity are all similar between the two environmental datasets (predicted breeding ranges are shown in Fig. 3 and SI Appendix, Fig. S11; partial ROC results are shown in SI Appendix, Table S8; environmental similarity is shown in SI Appendix, Figs. S8 and S12). Therefore, we reported the more conservative estimates of breeding range fluctuations in the main text based on the high-contribution dataset (Fig. 3). The ENMs based on the low-correlation dataset indicated more dramatic fluctuations in passenger pigeons' suitable breeding ranges. For example, using a threshold that allows for a maximum of 1% omission rate, the LIG range was 54-times LGM and current-day range was 87-times LGM (SI Appendix, Fig. S11).

Carrying Capacity Estimation. We defined passenger pigeon carrying capacity as the number of pigeons that could be sustained by annual acorn production. We estimated annual acorn production by multiplying modern-day

acorn production per square kilometer with historical oak coverage from 21,000 y before present to present day (inferred from fossil pollen records) for northern and eastern North America (47). For modern-day acorn production, we used the minimum, median, or maximum acorn production by red oaks or white oaks from published data collected across multiple sites and years (30, 31). Daily consumption of 30 acorns per pigeon was assumed (8, 38).

See *SI Appendix* for detailed methods.

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