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Point-of-view

Can genomic variation explain the extinction of the passenger pigeon?

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The passenger pigeon was once considered the most abundant avian species in the world. How its population dropped from billions to zero in mere decades is one of the biggest mysteries in conservation biology. In the past two decades, molecular methods have provided perspectives on population histories, although the time frames usually span thousands to hundreds of thousands of years. The extinction of the passenger pigeon in a few decades provides a rare opportunity to compare inferences from molecular data to the specifics of the population crash. From the period of 1800 to 1865, numbers of birds were estimated at 3–5 billion individuals (Schorger 1955). In 1869, market hunters from Van Buren County, Michigan sent 7.5 million birds to eastern markets. Shortly thereafter, upon completion of the eastern railroad network, probably every large breeding colony was within one day of travel for hunters. By the late 1870s, the last of the large nesting colonies was observed, which signaled an end to market hunting because it would be no longer profitable (Greenberg 2014).

The passenger pigeon likely survived by relying on predator saturation during the breeding season. After the toll exacted by market hunting, colonies would have been much smaller and therefore vulnerable to predation. In addition, sport hunting continued to have a role in reducing the population until 1900, when the last known wild specimen was harvested. The passenger pigeon thus went from a population estimated in excess of 3 000 000 000 individuals to extremely few from 1870 to 1900. It is unclear if this drastic population reduction would have had time to leave an indelible signature on genetic heterozygosity of the remaining birds owing to the low number of generations from peak population size to extinction.

We (Hung et al. 2014) analyzed genomic data extracted from three passenger pigeon specimens collected in 1879 ($n=2$) and 1881 ($n=1$), near the peak of the species abundance, and we concluded that passenger pigeons exhibited relatively low genomic diversity. In addition, we inferred that dramatic population fluctuations through its evolutionary history, especially population troughs, were responsible for the low genomic diversity. Murray et al. (2017) used genomic data from four passenger



pigeons (two of which were also used in our study, both collected in 1879, the other two collected in 1871 and 1880) to estimate the species' population history and concluded that natural selection had caused its low genomic diversity. Both studies therefore examined DNA from specimens collected near the peak population size, and before its dramatic decline, and would not likely exhibit bottleneck effects. Hedrick (2018) provided a population genetic analysis of Murray's et al. (2017) results, and we comment on additional aspects.

Murray et al. (2017) used both a coalescent approach (i.e. PSMC; Li and Durbin 2011) and nucleotide diversity (π values) to estimate the N_e of passenger pigeons at around 10^5 , much smaller than its peak census population size ($N_c = 10^9$). Their estimates are similar to Hung et al.'s (2014) estimated N_e (10^5) based on PSMC or G-PhoCS (Gronau et al. 2011). Murray et al. (2017) used another coalescent approach (i.e. BEAST; Ho and Shapiro 2011, Drummond et al. 2012) based only on mitochondrial genomes (mitogenomes) to show that N_e increased from 10^4 to 10^7 in the past 40 000 yr (Fig. 1B of Murray et al. 2017) and inferred from π values an average mitogenome N_e of 10^5 . This result is consistent with our estimates of nuclear genome N_e , and their result of a recent expansion in mitogenome N_e is consistent with our ecological niche models and analysis of the historical coverage of oak (the main food source of the passenger pigeon), which show the breeding habitat increasing since the Last Glacial Maximum (LGM, 21 000 yr ago; Hung et al. 2014).

Murray et al. (2017) claim that natural selection led to the passenger pigeon's low genomic diversity. They argued that the passenger pigeon genome shows stronger signals of natural selection than does that of the band-tailed pigeon *Patagioenas fasciata*. Murray et al. (2017) further assumed that the impact of selection could be widespread throughout the genome via linkage between genomic regions. However, selection should mainly work on coding regions and their nearby genomic regions (1000 Genomes Project Consortium 2012). Linkage (disequilibrium) cannot persist over long genomic regions or long time spans. Thus, the effect of natural selection on genetic diversity should be localized and cannot explain the overall low diversity of the passenger pigeon genome (Ellegren and Galtier 2016). In contrast, we believe that the relatively low N_e or small N_e/N_c of the passenger pigeon was mainly determined by demographic events, especially low points in population fluctuations, that would have had a genome-wide effect on genetic diversity because all regions in a genome share the same population history.

If Murray's et al. (2017) claim that natural selection had largely reduced the genome-wide genetic diversity of the passenger pigeon is correct, its mitogenome should have been subject to a similar or even stronger level of linked selection than its nuclear genome (Meiklejohn et al. 2007). Given that the mitogenome is a linked supergene including mostly coding regions, the genome-wide selective sweeps assumed by Murray et al. (2017) would likely have affected one or some proteins that are either coded by or associated with the mitochondrial genes and left strong signals in the mitogenome

(Hung and Zink 2014). However, Murray et al. (2017) show a larger N_e of the mitogenome than of the nuclear genome in the passenger pigeon during the past 30 000 yr. Thus, the contradictory patterns of N_e inferred from nuclear and mitochondrial genomes also do not support a strong effect of linked selection acting across the entire passenger pigeon genome.

Murray et al. (2017) showed the highly variable and uneven distribution of genetic polymorphism across the passenger pigeon genome and used it as evidence of natural selection. However, the uneven genetic polymorphism landscape does not necessarily reflect the impact of natural selection in the genome because genetic drift can also cause such a pattern (Manthey et al. 2015). The π values at the edges of chromosomes were up to ten-fold higher than other parts of chromosomes (Fig. 2B of Murray et al. 2017), which exceed differences found in other studies (Manthey et al. 2015). The results imply that parts of their estimated SNPs can be imprecise. Murray et al. (2017) argued that recombination and natural selection led to the highly variable polymorphism distribution of the passenger pigeon genome based on the pattern of higher recombination rates toward the telomeres in other avian genomes (Backström et al. 2010). In contrast, we believe that low genomic mapping quality at the edges of chromosomes in the passenger pigeon is a more likely reason. If high recombination rates at the edges of chromosomes are the reason, we should find similar patterns in the genomes of the band-tailed pigeon or other avian species; however, it is not the case (Ellegren et al. 2012; but see Manthey et al. 2015). Even though Murray et al. (2017) took some measurements to reduce the potential impacts of postmortem DNA damages on mapping and SNP calling, the efficiency of their approaches seems limited given the observed pattern. The potential mapping errors could influence the estimates of selection and population history in the passenger pigeon. Analyses based on multiple or more conservative mapping methods are required to test genomic mapping errors in the passenger pigeon sequences.

Murray et al.'s (2017) comparison of passenger pigeon and band-tailed pigeon is compromised by another, perhaps fatal flaw. A valid test of differences in the effects of selection requires comparison of recently diverged sister species. The passenger pigeon is the sister lineage to the New World pigeons in the genus *Patagioenas* (Fulton et al. 2012), a clade of nearly 20 species including the band-tailed pigeon. The depth of separation is well over five million years. Thus, the two species are anything but sisters, and inferences about the nature of selection resulting from comparison of these two species in its sister genera are irrelevant, both on phylogenetic and temporal grounds. A robust test would include all of the nearly 20 species found in the sister genus. Furthermore, one of the two band-tailed pigeon genomes used in this study was extracted from a captive-bred individual, and the inbreeding level in this captive bird and its impact on the selection tests are unknown. We conclude that no inferences about the nature of selection can be made from their comparison of passenger pigeon and band-tailed pigeon.

The passenger pigeon was driven rapidly to extinction from a population high point, and several factors were likely causal. Genetic data from specimens collected near the peak population size suggest either dramatic population size peaks and valleys over evolution (Hung et al. 2014) or elevated natural selection across genomic regions (Murray et al. 2017). Hung et al. (2014) also presented ecological niche models that were consistent with a period of very low population size in the passenger pigeon at the LGM. It is possible that the current genetic data, collected close to the population peak, do not clarify reasons for the extinction of passenger pigeons. Genetic data from specimens collected near the extinction event (e.g. 1900) might reveal whether population bottlenecks or natural selection caused major changes in the genetic variation of this bird (Díez-del-Molino et al. 2018). Even if natural selection had affected passenger pigeon genomes, the effective population size of species around 1870s was still around 10^5 , not a critically endangered size. Thus, genetic erosion caused by natural selection cannot explain the rapid extinction of the passerine pigeon.

It is likely that human over-harvesting reduced pigeon numbers to the point where their own breeding ecology, having enormous numbers of exposed flimsy nests, no longer protected them via predator saturation. Smaller and smaller colonies would have been increasingly vulnerable to predation and sport hunters, although Roberts et al. (2017) provide a contrasting view. Once at a critical low population threshold, lack of social stimulation and protection from nest predators doomed them to extinction. There is simply no reason to believe that slightly enhanced natural selection on some genomic regions reduced their genetic variation dramatically or made them more susceptible to extinction. Instead, the extinction event can be parsimoniously explained by the fact that it was the first time the species had encountered a super predator, humans.

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