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Evolution: A Genomic Guide to Bird Population History

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How species responded to the climatic oscillations during the past few million years is debated. A new study analyzing the genomes of 38 bird species finds variable patterns of population growth and declines that broadly correlate with global environmental change.

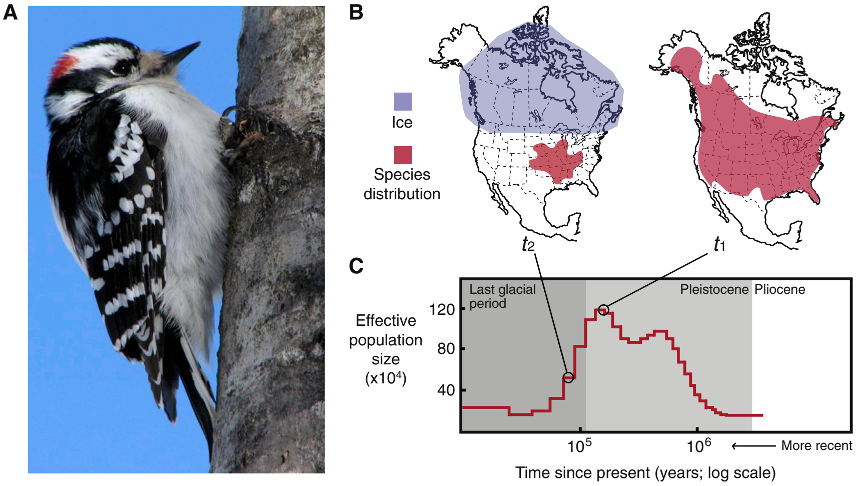
In a recent interview, Richard C. Lewontin, a central thinker in the field of evolutionary biology, succinctly noted that the ‘‘admission of necessary ignorance of historically remote things is the first rule of intellectual honesty in evolution’’ [1]. Possibly with reluctance, many biologists would admit to some level of ignorance in terms of our understanding of how different species responded to the extreme variation in climate over the past few million years. This is important, given that many of the species studied today presumably went through major shifts in their habitat and ecology during these times. Much of our understanding of the historical changes in the distribution and abundance of species have been gleaned from diverse sources, including fossils and pollen depositions [2]. Now, a recent paper in *Current Biology* by Nadachowska-Brzyska *et al.* [3] brings genomic data to bear on the question of how different species may have responded to these tumultuous times.

Extracting historical information from the genomes of extant individuals is a challenging affair. This is primarily because most methods used today provide only a snapshot of the recent past. For example, nucleotide variation in a species’ DNA can be used to indirectly estimate historical population sizes, whereby low levels of genetic variation suggest that its recent ancestral population was small. However, these statistics tells us little about what may have happened earlier — was this ancestral population preceded by a much larger group of individuals?

Recently, researchers have been able to work around these limitations by applying sophisticated modeling approaches to genomic data. These methods rely on the premise that different genomic regions within an individual’s DNA may provide semi-independent pieces of information from distinct historical time periods. One such analytical method that has become popular, pairwise sequentially Markovian coalescent modeling (PSMC), generates inferences about historical effective population sizes by using genome-wide sequencing data from a single individual [4].

Effective population size is a central metric in the field of population genetics: it considers only those individuals in a population that pass on genes to the next generation and, depending on the demographics, can be quite different from a population’s census size [3]. The PSMC framework was originally developed to quantify historical variation in effective population sizes in humans, although it has also been used to study patterns in pigs [5], horses [6] and other taxa [7]. In their study, Nadachowska-Brzyska *et al.* [3] mine 38 of the 48 recently published bird genomes [8] to quantify how population sizes of avian species changed globally over the past few million years. Avian systems, in particular, have a rich legacy of research into the patterns of diversity and historical biogeography [9,10].

The PSMC method employed by Nadachowska-Brzyska *et al.* [3] takes advantage of variation in the extent of heterozygosity (a simple measure of genetic variation) throughout the genome of diploid individuals. At this scale, heterozygosity can be influenced by a number of factors, but in this case it is assumed to be primarily affected by the effective population size. For



Current Biology

Figure 1. Shrink and expand.
(A) A male downy woodpecker (*Picoides pubescens*), one of the 38 avian genomes that Nadachowska-Brzyska *et al.* [3] analyzed (photograph by Peter de Wit; Wikimedia Commons). (B) A possible scenario for dynamic range shifts at high latitudes responding to glaciations by contracting (t_2) and then expanding (t_1) during more favourable times. (C) An example output of the PSMC analysis from Nadachowska-Brzyska *et al.* [3] showing variation in historical population size for the downy woodpecker through time.

instance, large populations will generally have higher levels of heterozygosity. This information is then combined with information about the coalescence time of each genomic region (i.e. the time to a common ancestor): each individual genome is a representative mosaic of its ancestors, and therefore different regions will coalesce at different times. The power of PSMC comes from combining information about heterozygosity and coalescence time: for different time periods in an individual's inherited history, one can indirectly estimate the effective population size of its ancestors. This metric then has the potential to look beyond the most recent past to estimate population variation at a deeper evolutionary history.

The inferences about population size extracted from the various avian genomes by Nadachowska-Brzyska *et al.* [3] encompass almost ten million years of history, up to the last ten thousand years — PSMC estimates are not reliable for much younger times [4]. While there is much variation across the taxa in this particular study, some notable patterns emerge. For instance, in many species there is a clear increase in estimated population size during the Pleistocene followed by steep declines, which are correlated with the last ice ages. For some species this corroborates our understanding of the species' biogeographic history. Downy woodpeckers (*Picoides pubescens*), for example, currently inhabit a large region of North America that was under massive ice sheets during parts of the Pleistocene [11]. It is therefore intuitive that this species would show a dynamic pattern of variation in effective population sizes, possibly corresponding to these dramatic climatic shifts (Figure 1). More puzzling perhaps are species that live in more stable environments. The sunbittern (*Eurypyga helias*), for instance, resides in lowland South and Central America [12]. It too shows a pattern consistent with population expansion and contraction during the past two million years. Even the well-studied medium ground finch (*Geospiza fortis*) on the Galapagos archipelago shows a similar signal of expansion and contraction. Contemporary census studies of this finch reveal wide inter-annual variation in population sizes [13], which may or may not be reflective of variation in the effective population size; yet, the fact that PSMC analysis captures this variation deep in its evolutionary history is notable. Taken together, these observations suggest that, while the environmental fluctuations during the Quaternary may have been more conspicuous at high latitudes, climatic oscillations clearly affected birds on a global scale.

These data also have some important implications for the conservation of living birds. The genomes for a number of species were originally sequenced due to their conservation status — six of the species are classified as endangered or vulnerable on the IUCN Red List of Threatened Species [14]. While many of the threats to these species arose because of relatively recent habitat alteration or hunting by humans, this new analysis suggests that many species were already showing a pattern of population reduction. For example, the endangered crested ibis (*Nipponia nippon*) had an estimated effective population size of 100,000 approximately one million years ago, but appears to have declined to approximately 2,000 individuals circa ten thousands years ago [3]. These findings imply that these taxa may have been already particularly vulnerable to anthropogenic influence.

There are a few caveats that suggest these population-size estimates will be likely to be refined in the future. For example, there are questions about how this method is affected by only sampling two haplotypes from a single individual and whether this kind of analysis can be scaled-up to population-level sampling. In addition, many of the interpretations rely on realistic estimates of mutation rate and recombination patterns, which are unknown for the taxa included in the study and therefore estimated indirectly. There is also heterogeneity in both of these parameters across the genome, whereas the method used by Nadachowska-Brzyska *et al.* [3] relies on a fixed estimate. Variation in these genomic characteristics would probably not change the overall conclusions of population expansion and contraction, but it could affect the interpretations of the relative timing and amplitude of changes in population size. Furthermore, this particular field is changing rapidly, and new methods are constantly being developed. In fact, a companion model to PSMC, multiple sequentially Markovian coalescent (MSMC), has recently been developed and purports to be more accurate at estimating population sizes within more recent divergence times [15].

New methods used to analyze genomic data, such as PSMC, are a rich resource for probing various questions, including the presumed effects of climatic fluctuations on various taxa. Indeed, while these data can only tell us so much, our ignorance of these remote historical times is ebbing. The study of Nadachowska-Brzyska *et al.* [3] represents thirty-eight small steps towards a more holistic understanding of how organisms have responded to environmental changes in the past. Hopefully the addition of new genomic data from many other species will provide an even more in-depth treatment of these important questions.

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Group Behavior: Social Context Modulates Behavioral Responses to Sensory Stimuli

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A new study reveals an unanticipated role for social context in driving group behavior of a solitary species to a sensory stimulus and is mediated by mechanosensory neurons signaling touch interactions among individuals.

A hallmark of the brain is that a singular input does not always elicit the same output; rather a given input might produce a variety of outputs depending on the current internal behavioral, and external states of the animal. This makes sense, as in order to generate a contextually appropriate behavioral response, an organism must not only objectively discriminate salient sensory stimuli from background noise, but also must assign value or valence to those stimuli, and it is these subjective evaluations that depend on the context or 'state' of the individual. While there exists a strong foundation of experimental and theoretical evidence across species for collective behavioral dynamics aiding in the navigation of sensory cues [1–3], we have a relatively poor understanding of the molecular and circuit machinery that drive such interactions. A recent study by Ramdya *et al.* [4] adds to the growing evidence for external state modulation of behavior by showing how social context modulates reactions to a characteristic sensory signal within the solitary vinegar fly *Drosophila melanogaster*.

Ramdya *et al.* [4] discovered a peculiar 'herd effect' in flies exposed to carbon dioxide (CO_2), which has been shown to drive a robust aversive escape response in walking flies [5,6]. To their surprise, they found that solitary flies only weakly avoid CO_2, and that only a group of flies strongly avoid the CO_2. This finding is broadly reminiscent of a classic study on human group behavior in which subjects were asked to take a written test. Smoke was