Avian seasonal reproduction in times of global warming

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Insights from evolution, ecology and (epi-)genetics

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Preface

The species that survived throughout the history of our ever-changing planet and shape the variation we observe today, are those species that adapted to changes in their environment via evolution. In "*On the Origin of Species*" (1859) Darwin outlined his theory of evolution by natural selection, defined by three main principles; (i) individuals within a population must show variation in the focal phenotype, (ii) parents and offspring must show resemblance in the focal phenotype and (iii) certain variants of the focal phenotype must favour individuals in the struggle of life. While the importance of evolution by natural selection was an early realization by Darwin and other contemporaries, most notably Alfred Russel Wallace, the process of evolution in big and complex species of wild animals was long thought to be too slow for humans to witness. Nowadays, however, there are many examples of evolution in action from wild study systems where species adapted to their changing world within human life-spans.

Among the earliest insights into the process of evolution in a wild animal species are derived from the long-term study of Darwin's finches on Daphne Major (Galápagos archipelago), initiated by Peter and Rosemary Grant in 1973. Darwin's finches proved most favourable for observing evolution by natural selection as the finches varied in their beak size, beak size was highly heritable and, especially under environmental change, individuals with certain beak size variants were more likely to survive. In short, the finches possessed all three essential ingredients for evolution by natural selection (Grant and Grant, 2003). For example, beak and body sizes of the medium ground finch (*Geospiza fortis*) showed pronounced heritability (Keller et al., 2001), varied within the population and determined which food resources a bird could access. There was a strong relationship between the ground finch's beak size and the maximum size and hardness of seeds a bird could crack (Schluter and Grant, 1984). During a severe drought in 1977, large and hard seeds dominated the food supply and, as a consequence, ground finches with smaller beaks, that lacked the mechanical power to crack the large and hard seeds, died at a higher rate. The selective survival in combination with the pronounced heritability of beak size, lead to an adaptive response to selection in the following generation; mean beak size of breeding pairs in the year of the drought was substantially larger compared to the mean beak size of breeding pairs in the year preceding the drought (1976). The adaptive response resulted in a substantial difference in mean beak size of offspring from 1976 and 1978. Eight years later, however, the Galápagos archipelago was subjected to a prolonged El Niño event from November 1982 to August 1983, leading to natural selection in the opposite direction. The abundant rain induced changes in vegetation and increased the availability of food, providing resources for vastly prolonged and highly productive breeding seasons in those years. When years of abundant rain were followed by a drought in 1985, competition for scarce resources was high, such that larger birds (that require more food resources to survive) died at the highest rate, leading to selective survival of medium ground finches with smaller body size and, this way, to an adaptive response towards smaller medium ground finches. While the droughts of 1977 and 1985 both induced strong selection pressures, selection oscillated in direction leading to differential adaptive responses. Throughout a 30-year period, oscillating selection was repeatedly observed (Grant and Grant, 2002), such that the ground finch did not remain morphologically constant or static, but repeatedly adapted to its changing environment. With their studies on the Darwin's finches, Peter and Rosemary Grant exemplified that evolution is observable in wild animal species and, moreover, provided an example of repeated adaptive evolution in response to oscillating environmental conditions showing that evolution is observable, interpretable and repeatable (Grant and Grant, 2003).

The ability of wild species to adaptively respond to changes in their environment has become more important for preserving our biodiversity than ever. Human activities have drastically impacted the planet and have led to rapid environmental changes that impose new selection pressures on wild species. A poster child example for an adaptive response to human-induced changes in the environment is the peppered moth (*Biston betularia*) in the United Kingdom (UK). The increased burning of coal in the UK during the start of the industrialization in the eighteenth century has led to a high soot pollution that blackened the three trunks, making the typica (pale grey) morph of the peppered moth conspicuous, while its melanic (dark) morph camouflaged well. As a consequence of higher birds predation of the typica morph (Cook et al., 2012), the melanic morph had a 50% survival advantage over the typica morph. From its first discovery in 1848, the frequency of the melanic morph rapidly increased with frequencies above 90% recorded in large parts of the UK by the 1950s. In the twentieth century, however, soot pollution decreased and the blackening of three trunks reversed, such that the frequency of the melanic morph started to drop in the early 1970s and decreased to less than 10% in large parts of the UK by the early 2000s (Cook, 2003). Overall, the peppered moth is one of the most recognized examples of evolution by selection, especially in the context of human-induced changes in the environment.

In addition to observing adaptive phenotypic responses to environmental change, scientists can now study the genetic basis of phenotypes under selection and the genetic origin of new variants. In the example of the peppered moth, breeding experiments have established that the alternative morphs are controlled by a single locus, with the melanic allele being fully dominant over the typica allele (Grant, 2004). Gene mapping of the melanic morph and a subsequent population genetic survey of UK-wide samples have shown that there was one core genetic variant, a single nucleotide polymorphism (SNP), that was associated with the melanic morph and carried signatures of recent strong selection (van't Hof et al., 2011). This association was found in all samples included in the survey, suggesting that the melanic morph in the UK was derived from a single ancestral haplotype and therefore has a single mutational origin. Revisiting the ground finch on Daphne major provides another example where a single locus was a strong driver of morphological divergences in response to selection. During a severe drought from 2004 to 2005, the medium ground finch was subjected to increased competition for food supply with the large ground finch (*Geospiza magnirostris*), resulting in selective mortality of medium ground finches with large beak sizes and a subsequent adaptive response towards smaller beak sizes (Grant and Grant, 2006). A genome-wide fixation index (F_{ST}) scan has identified several regions with strong differentiation and a diagnostic SNP (within the region that showed the strongest differentiation) carried signatures of strong selection in individuals that experienced the drought (Lamichhaney et al., 2016). These signatures of selection suggest that the F_{ST} outlier region played a significant role in the morphological divergence of the medium ground finch from the large ground finch. Both, the peppered moth and the medium ground finch, exemplify our ability to zoom into the genetic basis of phenotypes under selection and assess where in the genome selection took hold.

Overall, the medium ground finch and the peppered moth are two of the most recognized and influential examples in contemporary evolution that are now joined by many other species in which evolution by natural selection was observed - highlighting that evolution is a ubiquitous process. We now have the exciting opportunity to complement phenotypic observations from long-term study systems with molecular insights into the process of evolution; we can identify the genetic and genomic basis of phenotypes, the mutational origin of novel phenotypic variants and estimate signatures of selection on underlying genetic variants. Such molecular insights can be used to understand historical episodes of evolution by natural selection and, maybe more importantly, to predict evolutionary responses to future human-induced changes in the environment.

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