PNAS COMMENTARY

A yellow warbler is for the climate as a canary is for the coal mine

Peter R. Grant[a,1]

Bird populations are showing signs of being influenced by a warming climate. North temperate migrants are arriving on the breeding grounds earlier (1), upper altitudinal limits of some bird distributions are now higher (2), and a desert community of birds has collapsed (3). These ecological responses to climate change are well established, but do birds and other organisms show signs of an evolutionary response as well? The evidence is ambiguous. For example, a decline in average body size of 52 bird taxa in North America over 40 y is accurately predicted by increasing summer temperature (4), but such correlative studies by themselves cannot disentangle environmental and genetic responses to a changing environment (5, 6). The question of evolutionary change remains difficult to address and unanswered without long-term demographic studies of circumscribed populations (7) or experimental analysis of animals in captivity (8). An alternative tactic is to seek associations across a broad geographical range between genotypes, phenotypes, environmental variables, and proxy measures of fitness. This has been accomplished by Rodriguez and colleagues in a paper reported in this issue (9). A comprehensive study of the North American Yellow Warbler, *Setophaga petechia* (Spanish: *canario*), finds evidence of a failure of some individuals to keep pace with a changing environment. Populations of this species, it seems, are maladapted (10) to a changing environment. And if these are, then perhaps many other species are as well.

The authors present an argument in a stepwise progression. First, by capturing, measuring, and taking blood specimens from many individuals in Michigan, Pennsylvania, and elsewhere, they established genome-wide associations with variation in beak morphology. The loci are distributed across the genome, and several have previously been linked to craniofascial features of birds, so a functional connection with beak morphology is plausible. Second, by a similar analysis, the authors discovered environmental factors associated with putative selection on beak shape that they refer to as "drivers": They might equally well be called "punishers"! Precipitation (aridity) was found to be a key factor as it was in a massive analysis of 168 replicated studies of natural selection (11). The top four independent explanatory variables in the warbler study were precipitation of the warmest quarter, precipitation of the wettest quarter, precipitation of the driest month, and isothermality, which is a measure of the evenness of temperature across the year. In other words, environmental influences are not restricted to a single season.

Third, the question whether these associations reflect stress was addressed by using telomere length as a proxy indicator of stress. Telomeres are noncoding DNA sequences at the ends of chromosomes that protect coding DNA from erosion (12). Under stress, they shorten. To gauge the level of stress, the authors needed a comparison with populations of this species before the climate began to change in the 1950s, and here they were fortunate in having the results of a previous broad-scale survey of beak depth in relation to precipitation in the breeding season (13). If birds have the "wrong" beak dimensions for the current climate conditions, they would be expected to deviate from the historical relationship between beaks and precipitation. And that is indeed what the authors found. Telomeres were shortest on average in places that are now drier and where beaks are too shallow (small depth values) compared with the historical pattern. Having ruled out the possibility of a change in geographical distribution that might alternatively explain this result, the authors conclude that populations of this species are maladapted to their current climatic conditions. The suggestion of maladaptation—a lagging behind the optimal genotype in a changing environment (10, 14)—fits with a current decline in the species in parts of its distributional range (15).

Why should the depth (or height) of a beak be an indicator of stress? With seed-eating birds the ability to crack large and hard seeds is a function of beak depth (16). Warblers, by contrast, have long, thin, forceps-like beaks and feed largely on small insects and spiders by picking, pecking, and probing. Length rather than depth is likely to be the critical dimension. But beaks are more than tools for feeding, they are radiators of heat through the keratinized outer surface (17). The authors suggest one explanation for the link between precipitation and genetic variation in beak-linked loci of the warblers is that beak depth is important for simultaneously dissipating heat and retaining water in the hottest and driest areas where physiological stress, as indicated by relatively short telomeres, is greatest. Of interest is whether length (not measured) has remained unaltered subject to strong stabilizing selection for its feeding function while depth (and width?) is currently subject to directional selection for its physiological function; and whether a change in beak shape

Author affiliations: [a]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

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[1]Email: prgrant@princeton.edu.

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is facilitated by weak genetic correlations between the two beak traits.

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This paper is a bold effort to find a cryptic signal of fitness when it cannot be easily measured directly in unconstrained populations in the wild. It demonstrates a proof-of-principle in the detection of evolutionary change caused by climate change. Other workers confronted with similar problems in assessing evolutionary change will use telomeres, so it is important to be aware of limitations. First, telomeres shorten with age (7, 12, 18). They are considered biomarkers of senescence. Without an independent estimate of an individual's age, it will not be possible to unequivocally attribute short telomeres to the physiological stress of an extreme climate that is added to the normal stresses causing aging. Age and stress are confounded. In the case of the Yellow Warblers, for example, the shortening of telomeres associated with aridity may reflect a preponderance of old individuals in hot and arid environments. A demographic shift toward a top-heavy age distribution and low recruitment that this implies may nonetheless hint at difficulties in coping with environmental pressures including heat and aridity. Second is the challenge of identifying the salient traits responsible for the mismatch. This is a familiar problem in selection analysis when candidate traits related to fitness are intercorrelated, for then the task is to identify which one or more are causally related to the estimate of fitness (19). In the present study, beak depth in relation to body size is a plausible key morphological variable, but body size alone may be the crucially important component, especially in view of the likely physiological stress from heat and aridity. To carry this research forward, investigators might apply the same methodology for assaying fitness in relation to climate change to species where individuals can be repeatedly captured and their telomeres repeatedly measured, be they birds (7, 18) or other vertebrates (20).

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