Report

Cross-Generational Effects of Climate Change on Expression of a Sexually Selected Trait

Elizabeth S.C. Scordato,[1,*] Alexa L. Bontrager,[3]
and Trevor D. Price[2]
[1]Committee on Evolutionary Biology
[2]Department of Ecology & Evolution
The University of Chicago, Chicago, IL 60637, USA
[3]Section of Ecology, Behavior, and Evolution, Division of
Biology, University of California, San Diego, La Jolla, CA
92093, USA

Summary

Sexually selected traits and early breeding are often correlated with quality in birds: individuals that breed earlier in the season have more elaborate traits and raise more surviving offspring [1, 2]. As global climate warms, breeding date for many temperate birds is advancing [3, 4], but we lack corresponding information on climate-induced variation in sexual selection. Here, we investigated influences of climate on a sexually selected plumage trait in a Himalayan warbler (*Phylloscopus humei*). We found that when spring is warm, birds breed early. Subsequent to an early-breeding year, adults express relatively large sexually selected traits and rear offspring that also develop large traits. The positive effects of early breeding, plus the across-year correlation between parent and offspring cohorts, predict that warmer climates should lead to increases in trait size. However, trait size has not increased over the past 25 years, even though mean breeding date has advanced. We show that whereas warm springs have positive effects on trait size, warm summers have negative effects due to increased feather wear. Apparent stasis in the size of a sexually selected trait thus masks large, conflicting influences of climate change. Continued climate warming has the potential to affect the honesty of sexual signals, as trait expression and condition become increasingly disassociated.

Results

In seasonal environments, early breeding is an indicator of both parental condition and offspring investment: individuals that breed earlier in the season are in relatively good condition and express large sexually selected traits, and their offspring subsequently have relatively high survival [1, 2]. As global climate has warmed, avian breeding dates have advanced [3, 4]. However, warming spring temperatures frequently have negative, rather than positive, fitness consequences [5–7] due to phenological mismatches in species that do not appropriately adjust breeding date to match changes in the appearance of food resources [8, 9]. Corresponding studies of climate-driven variation in sexually selected traits are lacking, even though the condition-dependent nature of these traits means that they should be particularly sensitive to environmental heterogeneity [10, 11].

We have studied Hume's warbler (*Phylloscopus humei*), a small passerine bird, at three sites in the western Himalayas since 1985. Male and female *P. humei* have pale stripes, called wing bars, on their covert feathers, which have been shown to be subject to sexual selection ([12, 13]; Figure 1 inset). Wing bars develop in chicks within 3 to 4 days of hatching and can thus be influenced by in-egg maternal effects. The different timing of feather growth in chicks versus adults means that birds encode different aspects of environmental variation in their wing bars: adults molt their feathers in August, after breeding is completed, so their feathers are old when they are collected on the breeding grounds the following May. Wing-bar size in adults therefore depends on both feather development and feather wear. By contrast, chick feathers are collected at 10 days after hatching, so differences in wing-bar size reflect variation in feather development alone. To assess the impact of climate on wing-bar size, we used a large pedigree to (1) examine the relationship between adult and chick wing-bar size within and across years, (2) conduct quantitative genetic analysis to partition phenotypic variance within years into genetic and nongenetic components, and (3) analyze selection and parental effects to assess the relative role of these processes in driving trait variation across years. We then evaluated environmental effects on adult condition and wing-bar size and considered the potential for climate change to disrupt patterns of investment in these traits.

Variation in Adult and Chick Wing-Bar Size across Years

Across years, mean adult wing-bar size was correlated with mean chick wing-bar size (linear mixed model, with site included as a random effect to control for geographical variation; chick wing-bar size regressed on female wing-bar size: $t_{10} = 3.9$, $n = 14$, $p = 0.003$, Figure 1A; chick regressed on male: $t_{10} = 4.6$, $n = 14$, $p < 0.001$, Figure 1B; see also Figure S1 and Tables S1 and S2 available online). This association persists even though adult wing bars are worn and chick wing bars are fresh. A combination of developmental and environmental factors thus cause adult wing-bar size to vary across years, and this variation is transmitted to offspring. Cross-generation transmission of wing-bar size could occur either through fluctuating selection on genetically determined traits (with the shift in parental genetic mean equaling the shift in offspring phenotypic mean) or nongenetically, via differential parental investment. We assessed these alternatives by estimating quantitative genetic parameters for wing-bar size.

Quantitative Genetic Analysis of Wing-Bar Size

We constructed a pedigree with 1,817 individuals and used a restricted maximum-likelihood animal model to partition phenotypic variance in wing-bar size into additive genetic, common environment, and year components while controlling for effects of sex ([14, 15]; Supplemental Experimental Procedures). We found that wing-bar size was significantly heritable ($h^2 = 0.30$) and could thus respond to selection. Wing-bar size was also subject to a large, significant effect of common nest environment (11% of total variance; Table S3), which implies potential for within-year parental effects to influence chick wing-bar size.
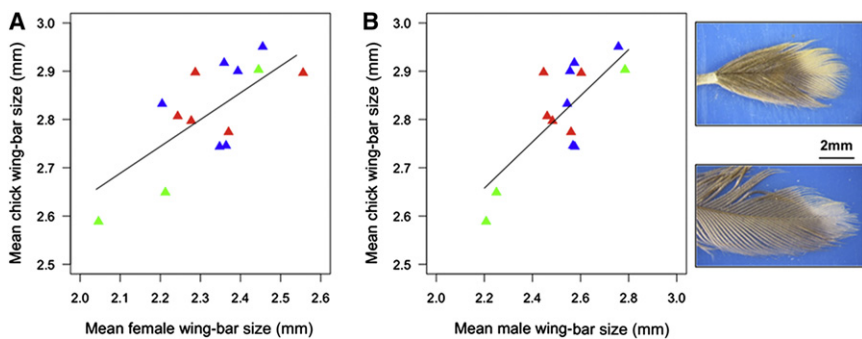
*Correspondence: escordato@uchicago.edu

Figure 1. Between-Year Correlation between Mean Adult and Mean Chick Wing-Bar Size

Data were collected at Overa (red), Manali (blue), and Keylong (green). Population mean chick wing-bar size for each year was regressed on mean female and male wing-bar size for the same year. See also Figure S1 and Tables S1 and S2 for statistics on annual variation in wing-bar size among years.
(A) Mean chick wing-bar size (average of nest means) regressed on female wing-bar size.
(B) Mean chick wing-bar size regressed on mean male wing-bar size. Inset: unworn chick (top) and worn adult (bottom) fourth greater covert feathers.

Selection Analysis

We conducted a retrospective selection analysis using the univariate breeder's equation [16] to estimate the intensities of selection required if the across-year fluctuations in chick wing-bar size are caused by genetic change alone. The strength of selection needed to produce phenotypic changes of the magnitude we observe in *P. humei* is stronger than most estimates of selection reported in nature [17]. Indeed, in 4 of the 7 years for which we could estimate the selection that would be required to cause the observed variation, truncation selection based purely on wing-bar size would require >50% mortality, much greater than is plausible (see Supplemental Experimental Procedures and Table S4). These estimates do not rule out some role for fluctuating selection in contributing to variation in chick wing-bar size, but genetic change alone clearly cannot explain all of the observed among-year variation; nongenetic factors must also be involved.

Analysis of Maternal Effects

Maternal effects are defined as influences of the maternal phenotype on offspring phenotype that occur beyond those due to genetic transmission [18, 19]. The maternal phenotype itself has genetic and nongenetic components, and thus the large nest effect we found in the animal model analysis is the result of three separate components of variance: genetic maternal effects, environmental maternal environment effects, and random effects of the nest environment. One way to estimate the full (genetic + environmental) maternal effect is to identify those maternal traits that directly affect offspring [20].

We compared regressions of offspring wing-bar size on mother's and father's wing bar to search for a direct effect of parental wing bar per se on offspring wing-bar size [20]. The maternal and paternal regressions were very similar (for genetic fathers: b = 0.18 ± 0.07, $F_{6,83}$ = 2.6, p = 0.02, Figure S2A; for mothers: b = 0.15 ± 0.05 SE, $F_{12,173}$ = 3.3, p = 0.0001, Figure S2A), and the slopes were not significantly different from each other (t test comparing the two slopes, t_{83} = 0.12, p > 0.1), implying no evidence for a maternal effect acting directly through the wing bar. We also found no evidence for a paternal effect, because the slope of the regression of extrapair chicks on foster father was not significant (b = −0.07, $F_{6,59}$ = 0.87, p = 0.41, Figure S2B) and was significantly smaller than the slope of males on their genetic offspring (slope given above; test for difference: t_{59} = 2.16, p = 0.03). The wing-bar size of males attending the nest therefore has no detectable effect on the wing-bar size of extrapair offspring.

Environmental Effects on Adult Wing-Bar Size

The across-year correlation that we observed between adult and chick wing-bar size (Figure 1) occurs even though we found no direct, within-year maternal effect. This implies that annual fluctuations in the environment lead to all females in a cohort adjusting investment in offspring wing bars in similar ways, with variation in investment among years being substantially larger than variation within years. In this scenario, in "good" years, all adults arrive on the breeding grounds in good condition, have large wing bars, and invest relatively more in their offspring, resulting in chicks with large wing bars. Conversely, in "bad" years, adults arrive to breed in poor condition, have small wing bars, and invest relatively less in their offspring, thus producing chicks with small wing bars.

We sought to identify climatic correlates of environmental quality. We studied two time points in the annual cycle during which environmental factors could affect adult condition and/or wing-bar size, (1) the previous year's breeding season and (2) the postbreeding molt. In many species, breeding early within a season is associated with high offspring and adult survival, implying that breeding early improves adult condition into the next year [2]. Climate-induced stress during molt has been linked to declines in the structural integrity of feathers [21] and can negatively influence feather ornament expression in other species [22].

We found that when spring was warm, the population bred early (see below). When the population bred early, both males (linear mixed model with site as a random effect: t_6 = 3.4, n = 9, p = 0.01) and females (t_6 = 2.3, n = 9, p = 0.06) arrived on the breeding grounds the next year with relatively large wing bars (Figure 2). In contrast, warm temperatures during the summer molt had negative effects on wing-bar size. Adults experienced more feather wear following warm summers (linear mixed model using mean temperature for June and July, with site as a random effect: t_8 = 3.9, p = 0.004, Figures 3 and S3). Moreover, increased feather wear resulted in smaller adult wing bars (correlation between adult wing-bar size and feather wear: r = −0.27, n = 64, p = 0.03).

Climate Change

We next asked how the observed effects of spring and summer climate on feather development and wear have been resolved over 25 years of climate change. Over this time, mean spring (April and May) temperature has warmed by almost 2°C in the western Himalayas ($F_{1,23}$ = 3.7, p = 0.07, n = 25, Figure 4A; [23]). Across years, mean breeding date is correlated with spring temperature (t_9 = 4.53, n = 13, p = 0.001, Figure 4B), and correspondingly, breeding date in our populations has advanced by about two weeks (t_9 = 2.9, n = 13, p = 0.02, Figure 4C). Although early breeding is correlated with large wing-bar size (Figure 2) and breeding date has advanced (Figure 4C), wing-bar size has not increased.
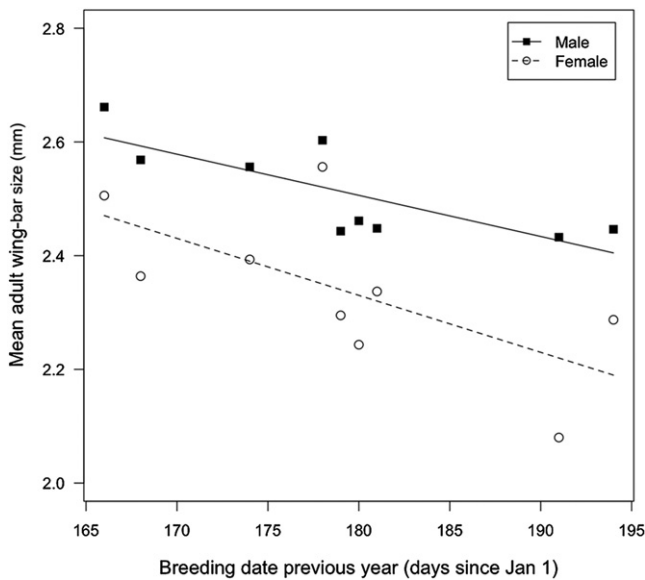
Figure 2. Relationship between Adult Wing-Bar Size and Breeding Date the Previous Year

Population mean wing-bar size for males (■) and females (○) regressed on population mean breeding date from the previous year, shown as days since January 1.
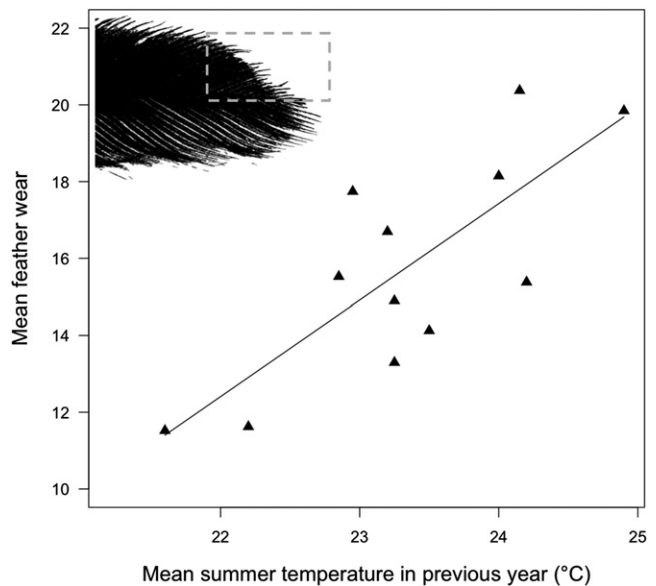

Figure 3. Mean Feather Wear Plotted against Mean June–July Temperature the Previous Year

Higher numbers are equivalent to greater feather wear. Inset: binary image of worn feather. The dashed rectangle designates the distal portion of the feather used in analysis of asymmetry. See also Figure S2.

Indeed, average chick wing-bar size shows a near-significant decline ($t_{11} = 2.11$, $n = 15$, $p = 0.06$, Figure 4D).

Discussion

We observed a striking correlation between chick and adult cohorts in a sexually selected plumage trait (Figure 1), which cannot be explained by fluctuating selection and genetic changes alone. Because we find no evidence of a within-year maternal effect, we conclude that variation in parental investment must be due primarily to annual factors that influence the entire adult population between years but cause relatively little variation among individuals within a year. Changes in mean phenotype across generations may be a result of either phenotypic plasticity or genetic evolution. Recent studies have found that although fluctuating selection in different environments is widespread [24–26], most instances of directional, climate-driven phenotypic change appear to be due to plasticity rather than genetic change [6, 15, 27, 28]. Our results are consistent with this pattern. Because phenotypic plasticity represents nongenetic change, it is largely a response to current environmental conditions that does not accumulate across generations. However, in systems with parental care, such as *P. humei*, response to different environments is transmitted across generations via differential parental investment and should therefore accrue over time, because the environments of previous generations influence the present phenotype [18].

We found that wing bars are larger after early-breeding years (Figure 2) and that breeding date has advanced by two weeks (Figure 4); we therefore expected wing-bar size to have increased over time. Instead, we found no directional change in wing-bar size, which we attribute to opposing effects of temperature at different time points. Early breeding and warm springs have a positive effect on adult wing-bar size (Figure 2) and likely lead to adults being in good condition.

Warm summers, by contrast, increase feather wear (Figure 3), thereby reducing wing-bar size and likely resulting in poor-condition adults. Spring and summer temperatures, although both exhibiting a trend toward increase over time [24], are not significantly correlated themselves ($r = 0.27$, $p = 0.20$), resulting in some dissociation of the two effects.

Our results highlight the contrasting effects that climate can have on the expression of sexually selected traits. For the wing bar, development and wear reflect environmental influences on different timescales. Feather development can only be influenced during the short window of feather growth. Conversely, wear is a continuous process that persists throughout the year. This means that birds that invest heavily in large wing bars during development but subsequently experience poor environments (and are unable to mitigate the negative effects) will return to the breeding grounds displaying small wing bars as a result of increased wear. In the western Himalayas, not only is climate warming [23], but both temperature [29] and rainfall [30] are becoming annually more variable. This trend will likely make it difficult for adult *P. humei* to appropriately allocate resources to both sexual advertisement and parental investment as environments become more unpredictable. Increased frequency of extreme climatic events and decoupling of previously linked phenological cues are consistent global patterns (reviewed in [31]), and *P. humei* is unlikely to be the only species facing problems with appropriate resource allocation in a changing environment.

Several studies have shown that environmental factors such as climate and population density drive population-level responses in morphological and life history traits [3, 32]. Corresponding demonstrations for sexually selected traits are rare ([22, 33, 34]) and have mostly been observed in human-altered systems [35]. Here we have shown that a sexually selected trait exhibits population-level plastic response to climate change. As climate becomes warmer, assuming that
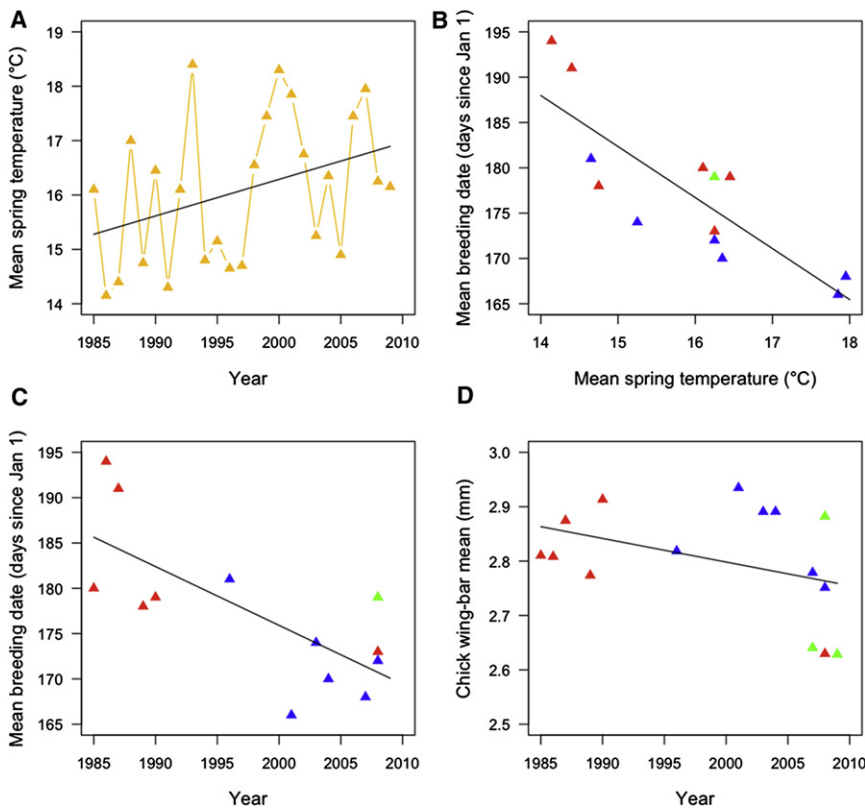
Figure 4. Changes in Breeding Date, Climate, and Wing-Bar Size over the Study Period

(A) Mean spring temperature in Srinagar exhibits a warming trend over the study period.

(B) Breeding date is significantly correlated with spring temperature. Data in (B)–(D) were collected at Overa (red), Manali (blue), and Keylong (green).

(C) Mean population breeding date has advanced over the study period.

(D) Mean chick wing-bar size shows a declining trend in recent years.

the trends we have identified persist, adults will suffer more annual wear in their wing bars while at the same time breeding earlier. A widespread feature of sexually selected traits is that they are correlated with condition, thereby signaling honest information about individual quality to receivers [10, 11]. Our results suggest that increased climate warming and climate variability can disrupt the information content of sexually selected signals in much the same as way as phenological mismatches disrupt the environmental cues used to initiate breeding behavior.

Supplemental Information

Supplemental Information includes three figures, four tables, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.11.044.

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