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Global Genetic Change Tracks Global Climate Warming in *Drosophila subobscura*

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Comparisons of recent with historical samples of chromosome inversion frequencies provide opportunities to determine whether genetic change is tracking climate change in natural populations. We determined the magnitude and direction of shifts over time (24 years between samples on average) in chromosome inversion frequencies and in ambient temperature for populations of the fly *Drosophila subobscura* on three continents. In 22 of 26 populations, climates warmed over the intervals, and genotypes characteristic of low latitudes (warm climates) increased in frequency in 21 of those 22 populations. Thus, genetic change in this fly is tracking climate warming and is doing so globally.

Climate change is altering the geographic ranges, abundances, phenologies, and biotic interactions of organisms (*1*, *2*). Climate change may also alter the genetic composition of species, but assessment of such shifts requires genetic data sampled over time (*2*–*5*). For most species, time series of genetic data are nonexistent or rare, especially on continental or global scales (*5*). For a few *Drosophila* species, however, time-series comparisons of chromosomal inversions are feasible (*4*, *6*–*8*) because these adaptive polymorphisms were among the first genetic markers quantified in natural populations (*9*). Consequently, historical records of inversion frequencies in *Drosophila* spp. provide opportunities for evaluating genetic sensitivity to changes in climate and other environmental factors (*4*, *8*, *10*, *11*). Time-series data (13 to 46 years, mean = 24.1 years) of chromosomal-arrangement frequencies and of climate are now available for 26 populations of the cosmopolitan species *D. subobscura* on three continents. Here we examine whether ambient temperatures have warmed at these sites and also whether genotypes characteristic of low latitudes have increased in frequency.

Drosophila subobscura is native to the Old World, where it is geographically widespread from North Africa to Scandinavia (*12*). It has a rich complement of chromosomal arrangements (inversions) on its five acrocentric chromosomes (*12*). Over the past half-century, inversion frequencies have been scored at many sites in the Old World. The frequencies of most inversions change clinally with latitude and thus with climate (*13*, *14*). These climatic clines must be maintained dynamically by natural selection because the gene flow within continents is very high (*15*). Therefore, temporal shifts in inversion frequencies should be sensitive indicators of adaptive responses to climate change (*4*, *10*, *11*).

In the late 1970s, *D. subobscura* was accidentally introduced (*16*) into South America and soon thereafter (*17*) into North America. It spread explosively on both continents (*18*). Geneticists soon (1981 in South America, 1985 to 1986 in North America) began surveying inversion frequencies of these introduced populations at different latitudes (*19*, *20*). On both continents they detected incipient latitudinal clines in chromosome inversion frequencies that almost always had the same sign with latitude as in the Old World, supporting the inference that these clines are adaptive (*18*, *21*). Some other traits of these introduced flies show rapid clinal evolution as well (*22*, *23*).

To obtain comparative data on contemporary chromosome-arrangement frequencies, we and colleagues have revisited many of the historical sampling sites in both the Old and New World. Initial studies with *D. subobscura* reported that "warm-climate" inversions have increased in frequency at several European sites and proposed that these shifts reflect climate warming, but these studies did not investigate continent-scale correlations with climate (*10*, *11*, *24*, *25*). Our analyses here investigate whether the magnitude and direction of genetic shifts actually parallel those in climate, and whether they do so on all three continents.

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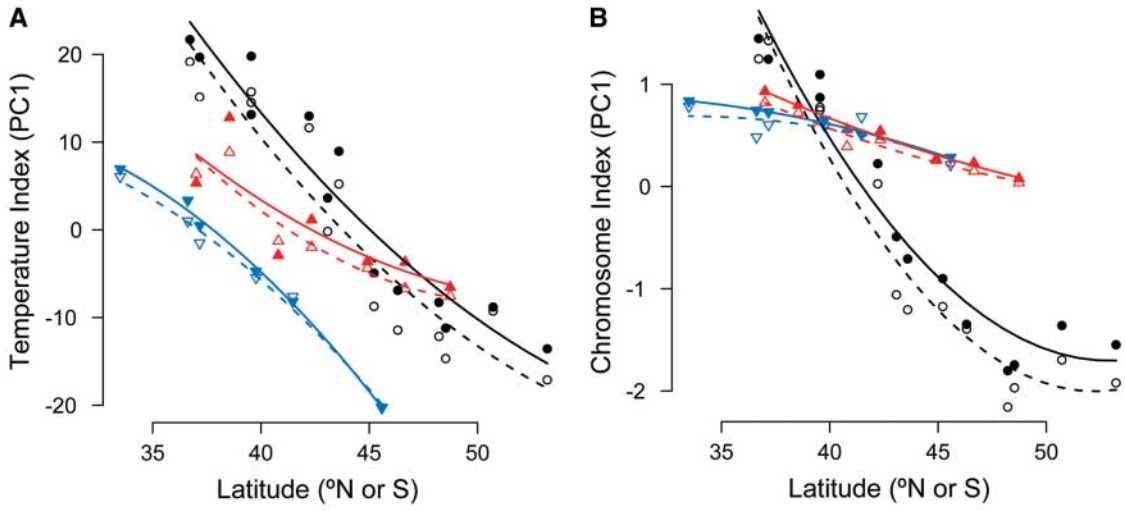

Fig. 1. Temporal shifts in temperature and in chromosome inversion frequencies at different latitudes on three continents. (**A**) A climate temperature index (T_{PC1}) is inversely correlated with latitude for 26 sites on three continents and has increased from the historical (open symbols, dashed regression lines) to contemporary samples (filled symbols, solid regression lines). Black, European sites; red, North American sites; and blue, South American sites. Regression lines are for second-degree orthogonal polynomials. (**B**) A chromosome index (Ch_{PC1}) is inversely related to latitude and has increased from the historical to contemporary samples (see text).

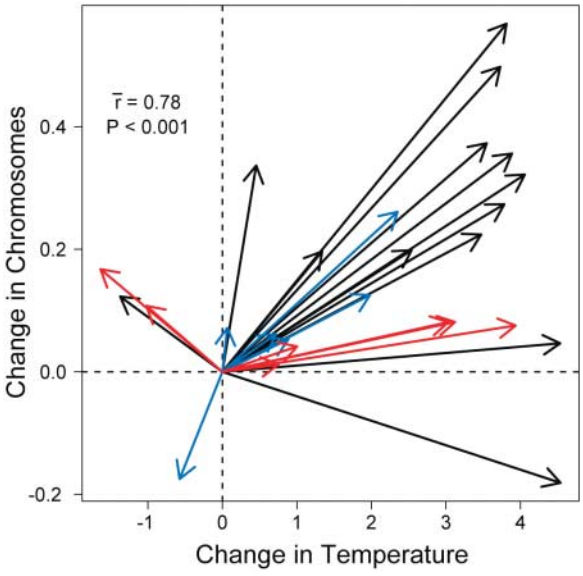

Fig. 2. Change in the direction of the chromosome index over time parallel those in the temperature index at 22 of 26 sites (upper right and lower left quadrants). Black, European sites; red, North American sites; and blue, South American sites.

Table 1. Spearman's rho correlation coefficients (95% confidence limits) for the relation between indices for chromosomes (Ch_{PC1}) and for climate (T_{PC1}) for old and for new samples on three continents. $^{**}P < 0.01$, *** $P < 0.001$.

Sample	Europe	South America	North America
Old	0.94***	0.49	0.93**
	(0.806, 0.982)	(−0.53, 0.930)	(0.584, 0.990)
New	0.95***	1.00***	0.93**
	(0.838, 0.985)	(1, 1)	(0.584, 0.990)

Table 2. Estimated equatorial shift (in degrees of latitude) between old and new samples from 10,000 bootstrapped replications of chromosome clines and of temperature clines. Values show means ± SE, with the 95% confidence limits indicated in parentheses.

Sample	Europe	South America	North America
Chromosomes	−0.884 ± 0.1721	−1.089 ± 1.4785	−0.757 ± 0.2612
	(−1.221, −0.547)	(−3.987, 1.809)	(−1.268, −0.245)
Temperatures	−1.106 ± 0.2095	−0.545 ± 0.1872	−0.735 ± 0.4275
	(−1.516, −0.696)	(−0.912, −0.178)	(−1.573, 0.103)

Historical data on inversion frequencies of *D. subobscura* in the Old and New Worlds were drawn from the literature (*11*). Between 1997 and 2004, contemporary estimates of inversion frequencies were scored from flies at the same (or very nearby) populations (*26*), during the same seasons as the original samples (*11*, *27*). Contemporary samples were also obtained in 2004 for seven populations in North America (*26*) (table S1). In all samples, each of the five acrocentric chromosomes was examined and scored for chromosomal arrangements, according to standard procedures (*26*). We analyzed 50 arrangements, including 21 that show significant latitudinal clines in the Old World and all 18 arrangements present in the New World (*27*).

Rather than analyzing frequency shifts of individual inversions, we developed a genome-wide index based on frequencies (p_i) of all inversions on the five acrocentric chromosomes. Specifically, we applied a principal component analysis to the centered and unscaled frequencies (after transformation by $2\sqrt{p_{ij}}$) of the scored arrangements on all chromosomes for the 52 (population × time) samples (*26*). Here we analyze the first principal component, which accounts for 45.8% of the variance.

To determine whether climates had shifted between samples at the study sites, we developed an index of ambient temperature. We compiled monthly mean temperatures from the nearest recorded weather station for the 4-year period before each sample and then computed a principal component index of the centered, unscaled monthly means for each site and period (*26*). The temperature index (T_{PC1}) reflects overall temperature and accounts for 79.8% of the variation.

T_{PC1} is inversely correlated with latitude on the three continents (Fig. 1A, table S2). Within continents, we found no significant heterogeneity among slopes between temporal samples ($F_{[4,17]} = 0.313$, $P = 0.865$), and so we used analysis of covariance to fit a common slope to

compute the between-sample effect (*28*). T_{PC1} increased significantly between samples ($F_{[1,\ 25]} = 28.8$, $P = 1.22 \times 10^{-6}$), consistent with global climate warming. Indeed, T_{PC1} increased at 22 of 26 sites. Shifts were larger in Europe (Fig. 1A), probably reflecting the longer sample intervals there and the broader range of climates (Fig. 1A).

A genomewide, principal component index of chromosome arrangement frequencies (Ch_{PC1}) was computed for all sites (*26*). Ch_{PC1} is inversely related not only to latitude (Fig. 1B, table S2), but also to T_{PC1} on all three continents (Table 1). Thus, Ch_{PC1} serves as a genetic indicator of the local climate. Because we found no significant differences in slope between temporal samples within continents ($F_{[4,17]} = 1.03$, $P = 0.419$), we fit a common slope within each continent and carried out an analysis of covariance (*29*). If the observed climate warming (Fig. 1A) is having a genetic impact, then genotypes associated with low latitudes (i.e., high Ch_{PC1} scores, Fig. 1B) should have increased in frequency between samples. In 24 of the 26 populations, this was indeed the case ($F_{[1,25]} = 22.7$, $P = 1.99 \times 10^{-6}$) (Fig. 1B). Within-site shifts in the direction of the chromosome index paralleled those of the temperature index in 22 of 26 sites (Fig. 2, sign-test, $P = 5.3 \times 10^{-5}$; Rayleigh test of uniformity, $\bar{r} = 0.78$, $P = 6.8 \times 10^{-8}$). Moreover, chromosome frequencies shifted toward a more low-latitude pattern in 21 of the 22 sites that warmed over the sample interval (upper right quadrant, Fig. 2). Thus, inversion frequencies have changed in step with climate on three continents.

In effect, genotype frequencies and climate at a given site have become more equatorial over the sample intervals (Figs. 1 and 2). Consequently, we rescaled the magnitude of these shifts (*26*) in terms of equivalent degrees of latitude (*4*). For temperature and for genotypes on all three continents, the observed shifts are equivalent to moving the historical sample site ~1° of latitude closer to the equator (Table 2).

Drosophila subobscura is experiencing detectable climate warming on three continents (Fig. 1A). Environmental warming appears to have had a genetic impact on these flies, because frequencies of chromosome inversions associated with warm latitudes have increased in parallel with climate on these continents (Fig. 2). This genetic shift is exceptionally rapid (*25*) and is detectable even for samples separated by fewer than two decades. Genetic shifts paralleling climate warming have been reported recently for a few other insects (*3*, *4*, *8*, *30*), although on more limited geographic scales. In no example to date, however, is it clear whether the observed shifts at given sites reflect local selection, a progressive invasion of genotypes from low latitudes, or both (*11*). Similarly, it is unclear whether the observed genetic changes reflect thermal (*8*, *31*) or seasonal selection (*5*), or correlates thereof.

The increasing numbers of examples documenting genetic (*2*–*5*, *8*, *10*, *11*), as well as phenotypic (*1*, *2*) responses, to recent climate change are not surprising from an evolutionary perspective, but nonetheless are disturbing from ecological or economic ones, because such changes signal inevitable disruptions in the distributions, population dynamics, and community interactions of organisms (*1*, *2*). Nevertheless, the ability of *D. subobscura* (*10*, *24*, *25*)—and probably other species with short generation times (*3*, *4*, *8*, *32*)—to respond genetically and rapidly to imposed environmental shifts may partially buffer their persistence in a globally warming world (*5*).

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Waking Experience Affects Sleep Need in *Drosophila*

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Sleep is a vital, evolutionarily conserved phenomenon, whose function is unclear. Although mounting evidence supports a role for sleep in the consolidation of memories, until now, a molecular connection between sleep, plasticity, and memory formation has been difficult to demonstrate. We establish *Drosophila* as a model to investigate this relation and demonstrate that the intensity and/or complexity of prior social experience stably modifies sleep need and architecture. Furthermore, this experience-dependent plasticity in sleep need is subserved by the dopaminergic and adenosine 3′,5′-monophosphate signaling pathways and a particular subset of 17 long-term memory genes.

Sleep is critical for survival, as observed in the human, mouse, and fruit fly (*1*–*3*), and yet, its function remains unclear. Although studies suggest that sleep may play a role in the processing of information acquired while awake (*4*, *5*), a direct molecular link between waking experience, plasticity, and sleep has not been demonstrated. We have taken advantage of *Drosophila* genetics and the behavioral and physiological similarities between