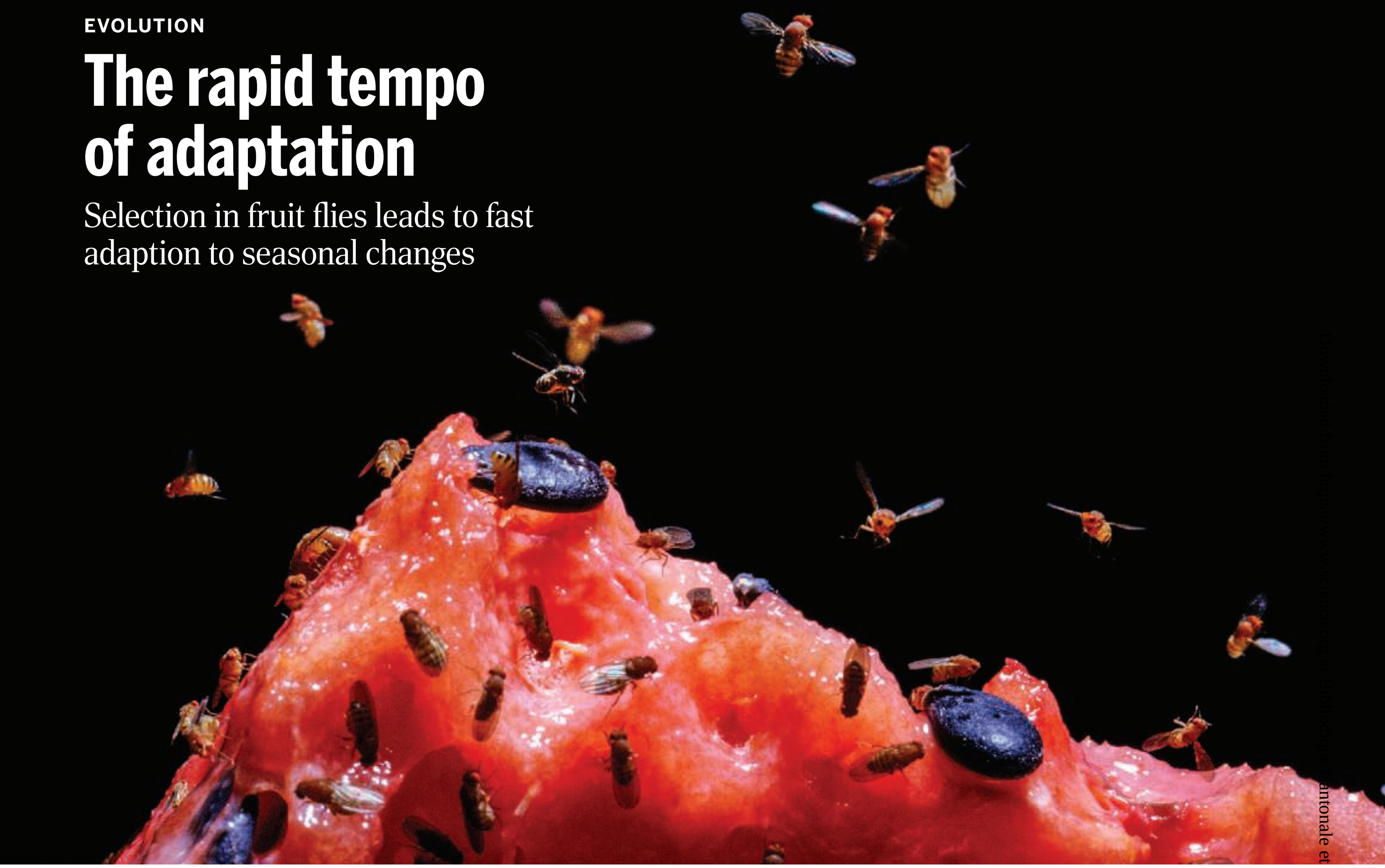
EVOLUTION

The rapid tempo of adaptation

Selection in fruit flies leads to fast adaption to seasonal changes



By **Ary H. Hoffmann**[1] and **Thomas Flatt**[2]

Understanding the tempo and mode of adaptive change is a long-standing problem in evolutionary biology (*1*). Although evolutionary dynamics are traditionally thought to be much slower than ecological changes, growing evidence shows that adaptation can occur at a pace comparable to that of ecological changes, as seen in Darwin's finches and other species (*2*). Fast adaptability is particularly important when organisms are facing rapidly changing environments. Populations can cope with these conditions either by evolving a "generalist" or an environmentally "plastic" phenotype, or by genetically and phenotypically adapting to each environmental change in what is known as "adaptive tracking" (*3*). Yet, classical theory predicts that adaptive tracking may be rare and unlikely to maintain genetic variation (*4*–*6*). On page 1246 of this issue, Rudman *et al.* (*7*) provide compelling evidence for seasonal adaptive tracking in field populations of *Drosophila melanogaster*—the fruit fly.

The fruit fly is a laboratory workhorse for examining the genetic basis of core biological processes. However, this unassuming insect has also played an important role in many ecological and evolutionary studies, including those on genetic variation in natural populations (*8*, *9*). This work and classical studies in ecological genetics, such as those on snails and moths, show how genetically determined phenotypes like wing morphs can mediate adaptation to environmental changes such as climate and predation (*10*). Rudman *et al.* build on findings in *Drosophila pseudoobscura* from the 1940s by geneticist Theodosius Dobzhansky, who observed seasonal fluctuations in the frequencies of chromosomal inversions in natural populations due to temporally varying selection (*11*). Contrary to classical theory, these and other studies suggest that selection is often sufficiently strong and variable across time to maintain different genetic variants (*6*), yet detailed empirical demonstrations of adaptive tracking are rare.

The study by Rudman *et al.* begins to fill this major gap between theory and observation and extends earlier work documenting changes in specific genetic markers and heritable ecological traits in fruit fly populations. The authors followed genomic changes in 10 independent replicate field cages of flies (100,000 per cage) exposed to changing weather across the season. In parallel, they documented monthly changes in quantitative traits after rearing flies in a "common garden" laboratory setting that is standardized to exclude environmentally induced and parental effects that would cause trait changes. The surveyed traits represent major components of fitness, including developmental rate and egg production, and three stress resistance traits: survival under cold, starvation, and desiccation. All of the observed fitness-related traits evolved in parallel among flies in all the cages, implying that selection and not random genetic change was responsible for trait evolution. However, the rate and direction of the phe-

[1]School of BioSciences, Bio21 Institute, University of Melbourne, Melbourne, Australia. [2]Department of Biology, University of Fribourg, Fribourg, Switzerland.
Email: ary@unimelb.edu.au; thomas.flatt@unifr.ch

PHOTO: SATOSHI KURIBAYASHI/MINDEN PICTURES

Research shows that fruit flies (*Drosophila melanogaster*) can adapt very rapidly to seasonally changing environments, in a phenomenon called "adaptive tracking."

notypic evolution varied depending on the trait. For example, chill coma recovery, an indicator of cold resistance, increased steadily toward winter, whereas desiccation resistance increased, then plateaued, and finally decreased. Notably, the rates of phenotypic evolution were extremely fast as compared to those seen in other animal species in the wild (*12*). Such a rapid evolutionary tempo is consistent with adaptive tracking, which requires maximal rates of evolution (*3*).

By testing for parallel changes in 10 replicate cages (each containing thousands of individuals), performing DNA sequencing for groups of 100 flies with a sequence coverage of >100-fold, and sampling every few weeks, Rudman *et al.* could detect temporal and parallel changes in the frequencies of gene variants (i.e., alleles) among replicates—a clear telltale of selection. As expected under strong fluctuating selection, many parallel frequency shifts changed direction over time. The genomic architecture underlying these changes indicates that many large blocks of the genome responded to selection, because of pervasive nonrandom associations between sites under selection with those unrelated to the selection response. This might reflect the use of experimental populations with only four generations of genetic recombination (i.e., the process that reshuffles gene variants) among the fly strains that were used to establish the populations. Thus, because recombination of DNA had a limited opportunity to break down these associations, the study cannot resolve fine-grained changes at small genomic regions. Despite this, the marked parallelism of the response to fluctuating selection represents strong evidence for seasonal adaptation through adaptive tracking. Further work is required to identify underlying causative changes.

An interesting aspect of the Rudman *et al.* study is the lack of evidence for inversions—when a segment of a chromosome is reversed—to be driving genetic changes. This seems to run counter to evidence for the importance of such rearrangements in rapid seasonal adaptation, as originally observed by Dobzhansky (*11*) and further supported by more recent studies (*4*). However, the frequencies of common inversions are quite low in natural *Drosophila* populations in Pennsylvania, where the flies used by Rudman *et al.* were from. This may help explain the lack of inversion contributions in their study. An open question is how the tempo and mode of seasonal adaptation depend on the populations of origin and their genetic makeup, including the prevalence of inversions.

Rudman *et al.* establish that fly populations can rapidly track seasonal changes. This might be expected on theoretical grounds as *Drosophila* populations are often very large with much genetic variation, and their evolution is not limited by rare mutations. Under such conditions, even weak selection can be effectively strong and drive a fast evolution. However, classical theories predict that adaptive tracking can be hindered by factors such as a reduction of fitness because of the time lag in adaptation after each environmental change, and other factors such as segregation load (fit heterozygous genotypes producing unfit offspring) and pleiotropy (genetic changes simultaneously affecting multiple traits that reduce fitness) (*3, 5*). Why these expectations are not borne out in real-world *Drosophila* populations remains unclear.

A recent comparison of genomic and quantitative genetic data suggests that balancing selection, possibly involving temporally varying selection, can contribute more to maintaining genetic variation than previously thought (*13*). In support of the underappreciated importance of fluctuating selection, previous genomic analyses have documented pervasive seasonal allele frequency changes in several fruit fly populations (*4*, *14*), and seasonal heritable changes have also been documented in flies for cold resistance (*8*). Emerging theories suggest that the conditions for fluctuating selection to maintain variability might be less stringent than previously assumed (*5*). The work by Rudman *et al.* lends strong credence to the feasibility of this mechanism and highlights the core issue (*15*) of how genetic variability can be maintained. ■

REFERENCES AND NOTES

1. G. G. Simpson, *Tempo and Mode in Evolution* (Columbia Univ. Press, 1944).
2. N. G. Hairston Jr. *et al.*, *Ecol. Lett.* **8**, 1114 (2005).
3. A. M. Simons, *Proc. Biol. Sci.* **278**, 1601 (2011).
4. H. E. Machado *et al.*, *eLife* **10**, e67577 (2021).
5. M. J. Wittmann, A. O. Bergland, M. W. Feldman, P. S. Schmidt, D. A. Petrov, *Proc. Natl. Acad. Sci. U.S.A.* **114**, E9932 (2017).
6. A. M. Dean, C. Lehman, X. Yi, *Genetics* **205**, 1271 (2017).
7. S. M. Rudman *et al.*, *Science* **375**, 1246 (2022).
8. A. A. Hoffmann, A. R. Weeks, *Genetica* **129**, 133 (2007).
9. J. R. Adrion, M. W. Hahn, B. S. Cooper, *Trends Genet.* **31**, 434 (2015).
10. E. B. Ford, *Ecological Genetics* (Chapman and Hall, 1975).
11. T. Dobzhansky, *Genetics* **28**, 162 (1943).
12. A. P. Hendry, T. J. Farrugia, M. T. Kinnison, *Mol. Ecol.* **17**, 20 (2008).
13. B. Charlesworth, *Proc. Natl. Acad. Sci. U.S.A.* **112**, 1662 (2015).
14. A. O. Bergland, E. L. Behrman, K. R. O'Brien, P. S. Schmidt, D. A. Petrov, *PLOS Genet.* **10**, e1004775 (2014).
15. R. C. Lewontin, *The Genetic Basis of Evolutionary Change* (Columbia Univ. Press, 1974).

10.1126/science.abo1817

ASTRONOMY

Unifying repeating fast radio bursts

Mysterious high-energy radio bursts are found to share certain characteristics

By **Manisha Caleb**

Indiscernible to the human eye, emanating from distant galaxies, are immensely energetic flashes of radio waves called fast radio bursts (FRBs) (*1*). These radio signals are both fast and explosive, releasing as much energy in a millisecond as the Sun releases over several days. Their transient nature, mysterious origins, and the sheer amounts of energy they exude on such short time scales make them fascinating. Most FRBs are one-off events, but a small subset has been observed to repeat (*2*). The diversity in the observed properties of FRBs has raised the possibility of differences even within repeating FRBs, especially displayed in their varying frequency and polarization characteristics (see the figure). On page 1266 of this issue, Feng *et al.* (*3*) present a unified characterization of repeating FRBs based on the frequency evolution of the FRB polarization.

Polarization is a fundamental property of electromagnetic waves and is typically used to probe the presence of magnetic fields. The rotation measure (RM) parameter quantifies the rotation of the electromagnetic waves by the foreground material they move through, whereas the polarization position angle provides information about the emission mechanism. Overall, polarization measurements of FRBs provide information about their origin as well as the immediate environment of the source producing them (*4*). Repeating FRBs offer astronomers the opportunity to study the polarization properties of FRBs in exquisite detail (*5*) with different telescopes and over various frequency ranges. Of all the known FRBs, few have had their polarization measured by astronomers. This is primarily because the data products are too large to be effectively stored and processed as a result of current computational limitations.

Sydney Institute for Astronomy, School of Physics, The University of Sydney, NSW 2006, Australia. Email: manisha.caleb@sydney.edu.au

The rapid tempo of adaptation

Ary H. HoffmannThomas Flatt

Science, 375 (6586), • DOI: 10.1126/science.abo1817

Science (ISSN 1095-9203) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.