

is special in two regards. First, it uses ultrafast laser pulses that are spectrally broad enough to excite all the relevant vibrational levels. Second, the spectrum is shaped to eliminate all frequencies that would excite from $v = 0$. As a result, molecules are trapped in $v = 0$, so after many incoherent cycles of excitation and decay, they accumulate in this “dark” state. Ironically, it is exactly this dark-state population trapping that has prevented traditional laser cooling of molecular motion. Here, it is put to good use: vibrationally cooling molecules that are already translationally cold.

Danzl *et al.* (3) also work with Cs₂ but use magneto-association of a Bose-Einstein condensate of Cs atoms to initially form the molecules. Rather than relying on broadband light to induce multiple absorption/emission cycles, they use a pair of laser beams with precisely defined frequencies to coherently drive the population from the initial state of high vibration, through an electronically excited intermediate state, then back down to a state of low vibration (see the figure). One difficulty with this process is the poor overlap of the wave functions of the highly excited and low-lying vibrational states. However, the lasers used for this two-photon process are locked to a frequency comb, and therefore highly coherent, allowing a long interaction time (10 μ s) and efficient transfer (80%) to the lower energy state. Danzl *et al.* can remove 0.13 eV of vibrational energy, which puts them one-fourth of the way to $v = 0$. They are optimistic

that by applying one more judiciously chosen two-photon process, they can reach the absolute ground state.

The technique used by Ni *et al.* on page 231 of this issue (4) is very similar to that of Danzl *et al.* but is applied to a rather different molecule, KRb. They report 56% transfer from the barely bound initial state to $v = 0$ of the lowest triplet electronic state, which is bound by 0.03 eV. Even more impressive is their demonstration of 83% transfer, using an intermediate state of mixed triplet-singlet character, to $v = 0$ of the lowest singlet electronic state. This is the absolute ground state of the system, bound by a whopping 0.52 eV. The fact that the KRb molecule is composed of two different atoms means that, as observed in this experiment, it possesses an electric dipole moment.

There is currently a great deal of interest in dipolar systems at low temperatures and high densities. Interactions between dipoles are both long range and anisotropic: Two dipoles oriented head-to-tail attract; side-by-side they repel. So, for example, a confined pancake-shaped sample will tend to be stable, whereas a cigar-shaped sample will tend to collapse. Such dipolar effects have begun to be observed in systems of magnetic dipoles (12), but the interactions will be much stronger between electric dipoles, enabling applications such as the modeling of complex many-body systems. Dipole-dipole interactions may also enable communication between cold molecule qubits in a quantum computer (13) and affect ultracold chemi-

cal reactions. For all these potential applications, a large dipole moment is desired. In states of high vibrational excitation, the atoms live far apart and the dipole moment is small; hence, the motivation for eliminating vibration.

Another compelling reason for going to the absolute ground state is a purely practical one: stability. All other states are unstable against inelastic collisions, which is a problem at high density. This recent progress toward populating the lowest-energy state therefore bodes well for producing a stable Bose-Einstein condensate or degenerate Fermi gas of molecules. Such systems will prove useful in exploring exotic quantum phases of matter and performing quantum simulations of highly correlated condensed matter systems.

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EVOLUTION

Armor Development and Fitness

William A. Cresko

Nearly 150 years after the publication of the *Origin of Species*, it is humbling to contemplate how well Darwin outlined the processes of evolution. The heritable basis of traits confounded him, however, and evolutionary biologists have since attempted to connect the processes of natural selection and genetic drift with the origin and distribution of genetic variation in the wild (1, 2). A flurry of recent work mapping phenotype to genotype has identified the molecular genetic basis of some traits in natural populations (3, 4), but documenting the fitness consequences of these genes has been more elu-

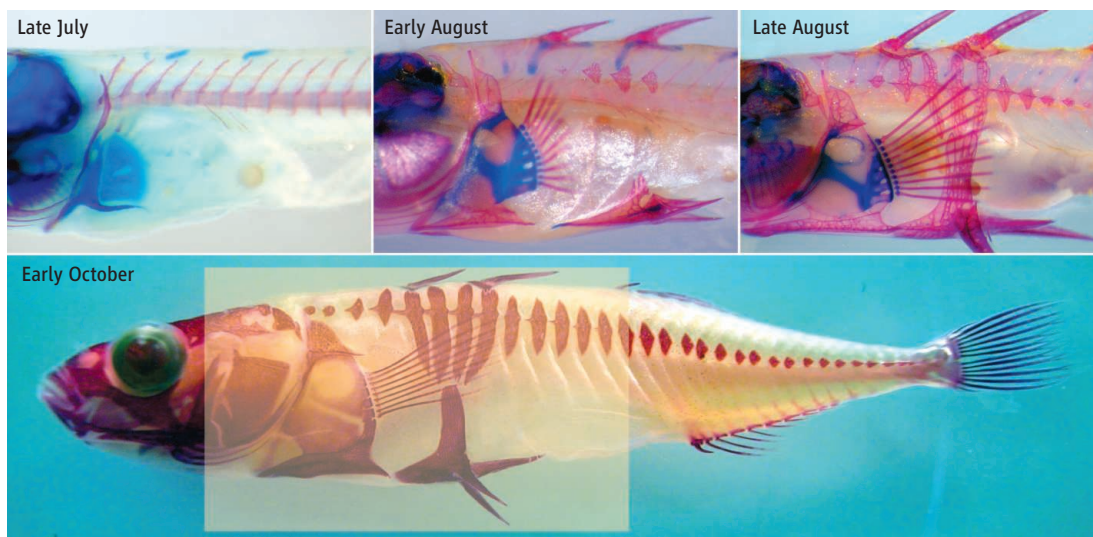
sive. An important study by Barrett *et al.* on page 255 in this issue (5) attempts to fill this gap by studying changes in allele frequencies in replicate populations of the threespine stickleback (*Gasterosteus aculeatus*), thereby adding an intriguing new wrinkle to a rapidly developing story.

Stickleback that originate in the ocean and subsequently become isolated in freshwater environments rapidly evolve the loss of external bony lateral plates (6). A major genetic factor on linkage group IV (the part of the genome corresponding to the largest stickleback chromosome) was implicated in this loss of armor in multiple populations (7, 8). “Low” alleles of the gene *ectodysplasin-A* (*Eda*)—which encodes a signaling molecule involved in ectodermal outgrowths such as hair, scales,

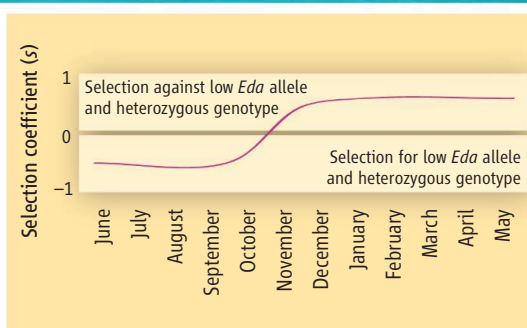
The fitness of stickleback fish that develop different numbers of external bony plates varies between oceanic and freshwater environments.

and teeth—were subsequently associated with the loss (9). Barrett *et al.* screened thousands of oceanic stickleback to find those heterozygous at the *Eda* locus—carrying one low and one “complete” allele, the latter of which encodes for the development of a full set of lateral plates. These fish were then introduced into freshwater ponds and quickly produced offspring that were sampled and genotyped at *Eda* throughout a full year (one stickleback generation). As expected, there was very strong selection (a selection coefficient of $s \sim 0.5$) for the low *Eda* allele in offspring fish that became large enough to have developed the complete set of plates (see the figure). This fitness differential could be due to the burden of forming and maintaining lateral plates, with the low *Eda* allele conferring higher

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Stickleback lateral plates. Approximate development of lateral plates in the threespine stickleback is shown for a fish born in early July: the absence of plates in late July; the formation of anterior lateral plates in early August; the formation of posterior lateral plates in late August; and the full complement of plates in early October. These stickleback are from a line grown in the laboratory, originally derived from a wild Alaskan oceanic population, and are used for illustrative purposes. The graph represents data from Barrett *et al.* showing selection against ($s < 0$), and for ($s > 0$), the low *Eda* allele and the heterozygous genotype, before and after fish develop a full complement of plates, respectively.



fitness in fresh waters because energy can be shunted away from bone formation and toward growth and reproduction (10). This “cost of plates” argument has intuitive appeal because freshwater stickleback populations at high latitudes need to endure many winter months, and increasing growth rate and sequestering energy could increase the probability of surviving the winter and reproducing early in the spring.

Despite the strong selection for the low *Eda* allele in older (larger) fish, selection was actually against this same allele before and during plate formation in young (smaller) offspring. Importantly, the selection coefficients against, and then for, the low *Eda* allele in young and older fish, respectively, were almost equal, a curious result considering the very rapid and nearly universal loss of plates once stickleback invade fresh waters (11). Barrett *et al.* hypothesize that *Eda* alleles may influence other phenotypic traits that are important for fitness before the plates fully develop. Alternatively, the change in *Eda* allele frequency in young fish may be a correlated response to selection of alleles of linked loci.

Freshwater habitats differ from oceanic ones in many conditions to which invading stickleback must adapt. Heterozygous fish were collected in the wild, and not created

through allelic introgression (the experimental addition of only the low *Eda* allele). Therefore, the genotype of the *Eda* allele may actually be a marker for haplotypes (genes closely associated on a chromosome that are inherited together) that contain *Eda* and numerous other genes in this region of linkage group IV. The linkage in a single haplotype of alleles at different loci subject to opposing selection could subsequently be broken through gene recombination during reproduction in the freshwater environment. Fixation of the recombinant low *Eda* allele-containing haplotype could occur due to the combined effects of selection for the low *Eda* allele and for a linked allele, producing the commonly observed rapid lateral plate evolution. Depending on the physical distance between linked genes on a chromosome and the recombination rate (the rate of exchange of DNA sequence between homologous chromosomes, thus forming new combinations of alleles), this pattern might be observed only after multiple generations. The linkage hypothesis makes the testable prediction that although many low *Eda* alleles may be present when a freshwater population is founded, a “hard” selective sweep for this region would involve only one or few recombinant haplotypes in any particular population (12).

of this genomic region and of the lateral plate phenotype. Amazingly, most of the present *Eda* low alleles that exist in stickleback populations around the world appear to be derived from a single allele that originated around 2 million years ago (9), and therefore most low alleles associated with lateral plate loss are likely identical by descent. Thus, the *Eda* alleles, and presumably other regions of the stickleback genome, have interacted in alternative oceanic and freshwater environments over very long periods, with potentially important consequences for the organization of genetic variation in the genome. A challenge for geneticists is to understand how evolutionary processes affect genetic variation in spatially explicit ways, both across geography and within genomes (14).

Despite these additional questions, the study by Barrett *et al.* is an excellent example of how experimental approaches can be used to link alleles to phenotypes and ultimately to fitness. Understanding the mechanistic basis of identified alleles in terms of cell behaviors, developmental trajectories, and physiological systems (15) may help to explain how intermediaries in the genotype-to-phenotype map might influence the distribution of phenotypic variation in new environments or lead to pervasive parallel evolution such as that seen

in stickleback. The study by Barrett *et al.* points to the great promise for connecting molecular genetics with phenotypic variation and fitness in the wild, a synthesis that would have made a pleasant gift for Darwin on his 200th birthday next February.

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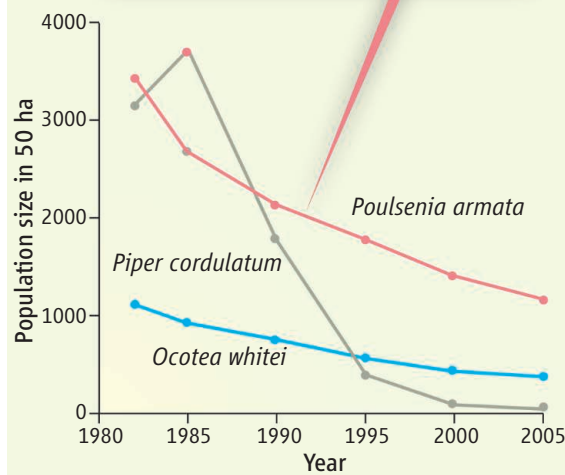
ECOLOGY

Biodiversity in a Warmer World

Jens-Christian Svenning¹ and Richard Condit²

There is ample evidence that 20th-century warming has shifted ranges of temperate and arctic species, but on page 261 of this issue, Moritz *et al.* (1) provide an exceptionally thorough example: They take advantage of a well-documented study from a century ago (2) to demonstrate contractions and expansions of elevation range among small mammals in Yosemite National Park, California, USA. In contrast, there have been few attempts to even address the tropics' sensitivity to global climate change (3). Also in this issue (page 258), Colwell *et al.* (4) use a novel conceptual approach to analyze climate shifts in tropical ecosystems.

Colwell *et al.* explain that weak latitudinal temperature gradients in the tropics will make it difficult for species to track suitable climatic conditions by migrating through the lowlands; instead, short-distance upslope migration to cooler mountains is what we should expect. The authors note three ways in which global warming may cause extinction. First, the tropical lowlands may experience biotic attrition: Warming drives species out of the lowlands, but no source of species adapted to higher temperatures is available to compensate the losses. The two additional risks for tropical mountain species are range-shift gaps (where species' current altitudinal ranges do not overlap climatically suitable ranges of the future) and mountain-top extinction (where warming pushes climatically suitable conditions off mountain peaks). These latter risks are also relevant outside the



Steep decline. In a complete census of trees above 1 cm diameter in 50 ha of forest in Panama, the largest population declines are associated with drought, not temperature change (13).

tropics (5); indeed, Moritz *et al.* document the contraction of ranges of high-elevation species in Yosemite.

Colwell *et al.* then analyze ranges of 2000 species of plants and insects along a 2900-m altitudinal transect on Volcán Barva, Costa Rica, and relate these to expected upslope climate shifts. They find that a 3.2°C warming threatens 53% of the species with lowland extinction and 51% with range-shift gaps. Only a minority of species would face mountain-top extinction.

These numbers suggest large risks. However, the figures are likely to be controversial, because there are substantial uncertainties in our understanding of the sensitivity of tropical species to climatic warming. Notably, the prediction of heavy lowland extinctions is based on the assumption that species will be unable to tolerate temperatures higher than today's. Yet, many extant species evolved when climates were warmer (6) and may retain this warmth tolerance. Climatic limits within lineages often remain remarkably stable over millions of years (7, 8). On evolutionary time scales, there is little evidence that warming is detrimental in the tropics: Neotropical plant diversity peaked in the period of maximum warmth between 35 and 55 million years ago (9), and high tropical diver-

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