CLIMATE CHANGE

Evolutionary Response to Rapid Climate Change

William E. Bradshaw and Christina M. Holzapfel

ver the past 40 years, species have been extending their ranges toward the poles and populations have been migrating, developing, or reproducing earlier in the spring than previously (1-4). These range expansions and changes in the timing of seasonal events have generally been attributed to "phenotypic plasticity"—that is, the ability of individuals to modify their behavior, morphology, or physiology in response to altered environmental conditions (5, 6). Phenotypic plasticity is not the whole story. However, recent studies show that over the recent decades, climate change has led to heritable, genetic changes in populations of animals as diverse as birds, squirrels, and mosquitoes (see the first figure).

These genetic changes in animal populations (7) have involved adaptation to the timing of seasonal events or to season length. For example, Canadian red squirrels are reproducing earlier in the spring, thereby capitalizing on earlier spruce cone production (8). Blackcaps (birds) in central Europe have been increasingly overwintering in Britain rather than Iberia; the genetically distinct British subpopulation arrives earlier at the nesting grounds and thus obtains superior territories or mates (9, 10). European great tits (birds) depend on caterpillars to feed their young. With earlier springs, the caterpillars have been maturing earlier, before the tit chicks hatch, leading to a decline in lifetime reproductive success of the birds. Among the tits, there is genetic variation in the ability to adjust egg-laying date. The individual birds most able to modify the timing of egg laying in response to the earlier springs are the ones that maintain the greatest lifetime reproductive success (11).

Insects are also adapting to recent, longer growing seasons. In European (12), North American (13), and Australian (14) populations of fruit flies, the frequencies of different alleles and of chromosomal inversions have been shifting toward the frequencies of more southern populations. With longer growing seasons, populations of North American mosquitoes that live in pitcher plants have shown a genetic shift toward the use of shorter, more southern day lengths to cue the initiation of larval dormancy (15).

Although the specific adaptations of these animals to climate change are as diverse as the organisms themselves, they all involve genetic

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Recent, rapid climate change is driving evolution, as organisms adapt to altered seasonal events rather than to the direct effects of increasing temperature.



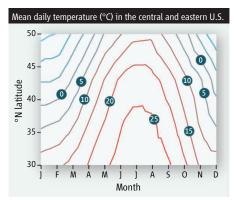




Adaptive animals. The Yukon red squirrel (Tamiascurus hudsonicus) (left), the pitcher-plant mosquito (Wyeomyia smithii, shown descending into its carnivorous host, Sarracenia purpurea) (middle), and the European blackcap (Sylvia atricapilla) (right) show genetically based shifts in the timing of their seasonal reproduction, dormancy, or migration during recent, rapid climate warming.

changes relating to season: earlier or more flexible timing of reproduction in squirrels and birds, later arrival of winter in mosquitoes, and a longer growing season for fruit flies.

None of these studies provides evidence that there have been genetic changes in response to higher temperature alone. Moreover, when northern mosquitoes were experimentally transplanted to a simulated southern climate, a huge loss of fitness occurred; 88% of this fitness loss was due to experiencing the incorrect seasonal cues (day length), whereas the warmer summer temperature of the more southern locality was not a factor (16). Hence, the correct interpretation of cues that correspond to seasonality, rather than to hotter temperatures, is of primary importance. We



Winter cold versus summer heat. The isotherms for mean daily temperature in the central and eastern United States (from the Gulf of Mexico to the Canadian border) are close together in the winter but spaced far apart in the summer. Thus, changes to seasonal length or the timing of spring have a greater effect on animal populations than changes in temperature by themselves. Data are for 1931-1960 (16), before rapid climate warming occurred.

are not aware of any examples of genetic changes in animal populations toward either higher thermal optima or greater heat tolerance that are correlated with recent climate warming.

A consideration of the seasonal profiles of temperature in eastern and central North America shows why recent climate change is imposing seasonal rather than thermal selection on natural populations (see the second figure). The latitudinal variation in climate is less a matter of summer warmth (the July isotherms are far apart) than it is of winter cold (the January isotherms are close together), and northern populations experience shorter growing seasons than southern populations. For example, mean daily temperatures are above 10°C all year at 30°N but are above 10°C for only 2.5 months at 50°N. Global warming is proceeding fastest at the most northern latitudes, where the gradient in winter cold is steepest (17, 18), thereby expanding the growing season while alleviating winter cold stress without imposing summer heat stress (16). Hence, northern climates are becoming more like those in the south.

At least within insect species, northern populations use longer day lengths to cue the initiation of dormancy earlier in the fall than do southern populations (18), and recent climate warming has resulted in a genetic shift toward the use of shorter, more southern day lengths (16). By contrast, within insect species, the upper limits of heat tolerance do not change with latitude (20), because the latitudinal variation in North American surface temperature is more a matter of winter cold than of summer heat (see the second figure). Hence, adaptive shifts in the timing of seasonal events should precede adaptive shifts of

thermal optima or increased heat tolerance over evolutionary time, and that is the pattern that is emerging.

Studies providing evidence for genetic change in response to recent, rapid climate change have come from research groups that have focused their efforts on one or a few species over several decades. These studies have involved retrospective comparisons in flies, mosquitoes, and blackcaps or have used pedigree analysis through multiple generations in squirrels and great tits. The time scales over which genetic changes are detectable cover a wide range. In mosquitoes, a clear change could be seen over 5 years (15). Moderate changes were detectable over 10 years in red squirrels (8). In great tits, even after 30 years, only the portion of the population that is most able to modify the timing of egg laying in response to earlier springs has changed genetically (11). Despite both phenotypic and genetic changes in the ability of great tits to track the seasonal availability of caterpillars, the average lifetime reproductive success of the population as a whole is declining. The population cannot keep pace with environmental change and may be vulnerable to extinction (11). Hence, the ability to evolve in response to recent climate warming does not, in itself, ensure that a population will survive (2, 11, 21).

As these examples show, the effects of rapid climate warming have penetrated to the level of

the gene in a diverse group of organisms. These genetic changes in populations affect the timing of major life history events: when to develop, when to reproduce, when to enter dormancy, and when to migrate. Small animals with short life cycles and large population sizes will probably adapt to longer growing seasons and be able to persist; however, populations of many large animals with longer life cycles and smaller population sizes will experience a decline in population size or be replaced by more southern species. Questions remain about the relative rates of environmental and evolutionary change (5, 11, 21, 22). But it is clear that unless the long-term magnitude of rapid climate change is widely acknowledged and effective steps are taken to mitigate its effects, natural communities with which we are familiar will cease to exist (2, 22-24).

References and Notes

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APPLIED PHYSICS

Toward Robots That Can Sense Texture by Touch

Richard Crowder

anday's state-of-the-art dexterous robotic hands cannot achieve tasks that most 6-year-old children can do without thinking, such as tie a shoelace or build a house of cards. The improvement of the manipulative capabilities of robotic hands requires advances in a wide range of technologies, including mechanics, actuators, sensors, and artificial intelligence. Many robots—such as NASA's Robonaunt (1)—have the dexterity required to perform some of the tasks that we take for granted, but replication of the full manipulative capabilities of the human hand is still years away.

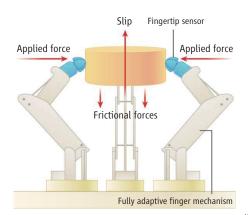
A key advance needed for these new robots is the development of a sensor or set of sensors that can replicate the human sense of touch. Most robotic systems incorporate binary touch

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sensors—that is, sensors that can distinguish between touch or no touch. Many more sophisticated sensors have been discussed in the literature, but their take-up by industry is hampered by manufacturing challenges, in particular, the assurance of protection against the wear and tear found in the real world. In contrast, vision sensors are almost commonplace in many robotic systems (2).

The development of tactile sensors is one of the most difficult aspects of robotics. (A tactile sensor measures force and spatial information, whereas touch is technically just the force at a single point.) Many technologies have been explored, including a carbon-loaded elastomer, piezoelectric materials, and micro-electromechanical systems (3). Many designs exist, but few have moved from the research laboratory to become a commercial success. Those that have tend to be robust and easy to construct, but provide poor spatial resolution.

A compact, high-resolution touch sensor has been developed from a thin film. Incorporation of this sensor into robotic hands may substantially improve their dexterity.



A three-fingered gripper. The fingertips are designed to allow a wide variety of objects to be grasped and manipulated. The addition of a fingertip sensor will not only allow the applied force to be controlled, but will also (with a suitable controller) minimize the object's slip in any direction.

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