

Fight hard, die young. Male-biased mortality is well established in mammalian species. Male savannah baboons have a much higher mortality rate than females and also are much more susceptible to parasitic diseases. The susceptibility of males to parasitism may reflect their greater size or male-male competition for mates and territory (10).

are more than four times as vulnerable to parasite-induced death. Furthermore, the increase in male-biased mortality is not simply associated with puberty, but typically occurs later in life (see the second figure). Together with Moore and Wilson's study of nonhuman mammals, these data suggest that differences between males and females in "immunocompetence"—an organism's all-round ability to avoid the harmful effects of parasites—may underlie the increase in male-biased mortality.

The classic explanation for low immunocompetence in male mammals is that masculinization depends on testosterone, an immunosuppressant (4). Long-term comparisons between castrated and "intact" men show that the former outlive the latter by up to 15 years. The life-prolonging effects of castration are proportional to the age at which the operation was performed (5). Moreover, because these comparisons have typically been based on institutionalized populations, the elevated rate of mortality among intact males is usually due to infectious diseases rather than violence or accidents.

The exact mechanisms by which testosterone causes immunosuppression are still under investigation. One possibility is that testosterone alters the way in which males allocate resources among competing needs. Males may be unable to mount an effective immune response because they face a trade-off between allocating resources to fending off disease and allocating resources to other activities. The most obvious resource is energy itself and, given the huge number of cells involved in immune defense, it is plausible that a prolonged response would be energetically costly. However, there could be trade-offs

with respect to other scarce nutrients, such as carotenoids, which are important not only in many basic metabolic pathways but also for effective operation of the immune system (6). Alternatively, trade-offs may occur indirectly—for example, intense metabolic activity could lead to immune system damage caused by the release of free radicals (7). It has even been suggested that the reduced immunocompetence of males may be an adaptive response, which minimizes the risk that the male immune system will produce autoantibodies, as happens during autoimmunity (8). The relative likelihood of these different mechanisms has not yet been established.

It is worth remembering that the sex differences in susceptibility to parasitism may not reflect "maleness" per se. Indeed, Moore and Wilson (2) show that, in species where females are larger than males, it is the females that suffer the greater burden of parasitism. In other words, males are not special, they just tend to be big. This counterintuitive result highlights one of the great difficulties in interpreting results based on the incidence of parasitism: Variations between individuals may be due to differences in exposure to parasites rather than differ-

ences in resistance to parasites. Thus, in the context of sex differences in parasitism among mammals, males may simply offer a bigger "target" to parasites because they are big and eat a lot. Again, some human studies support this view, with one showing that women were more vulnerable to some nematode infections simply because they did most of the washing and thereby were more frequently exposed to the infective stage of the parasite (9).

The next step is to discover more about the precise physiological mechanisms that lead to the unusually high susceptibility of large mammals to parasitic diseases. Is this susceptibility due to a shortage of energy or a scarcity of nutrients, or is it simply because of a greater exposure to the parasites?

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PERSPECTIVES: ECOLOGY

Quaternary Refugia and Persistence of Biodiversity

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Preserving biodiversity represents a daunting challenge for human societies. Ideally conservation policies should be based on sound scientific data, including an understanding of the mechanisms that sustain biodiversity over long periods of time. On page 2044 of this issue, Tzedakis *et al.* illustrate the importance of southern refugia for the persistence of some temperate tree species during the last glacial-interglacial cycles (1).

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The Milankovitch theory of climates, relates the glacial-interglacial cycles to changes in Earth's orbital parameters during the Quaternary period (the last two million years). These long-term parameters are orbital eccentricity, obliquity, and precession, with periods of 100,000, 41,000, and 19,000 to 23,000 years, respectively (2). Superimposed on the long climatic cycles are short and abrupt climate changes caused by the complex relationships between solar energy, vegetation, and the oceans. For example, in the North Atlantic Ocean, cold climatic cycles of about 10,000 to 15,000 years duration correspond to shifts in the ocean-atmosphere temperature (3). These short cycles culminate in huge discharges of icebergs into the North Atlantic Ocean (Heinrich events) (4) that are followed by an abrupt shift to a warm climate. Both the long-term and the short-term climatic varia-

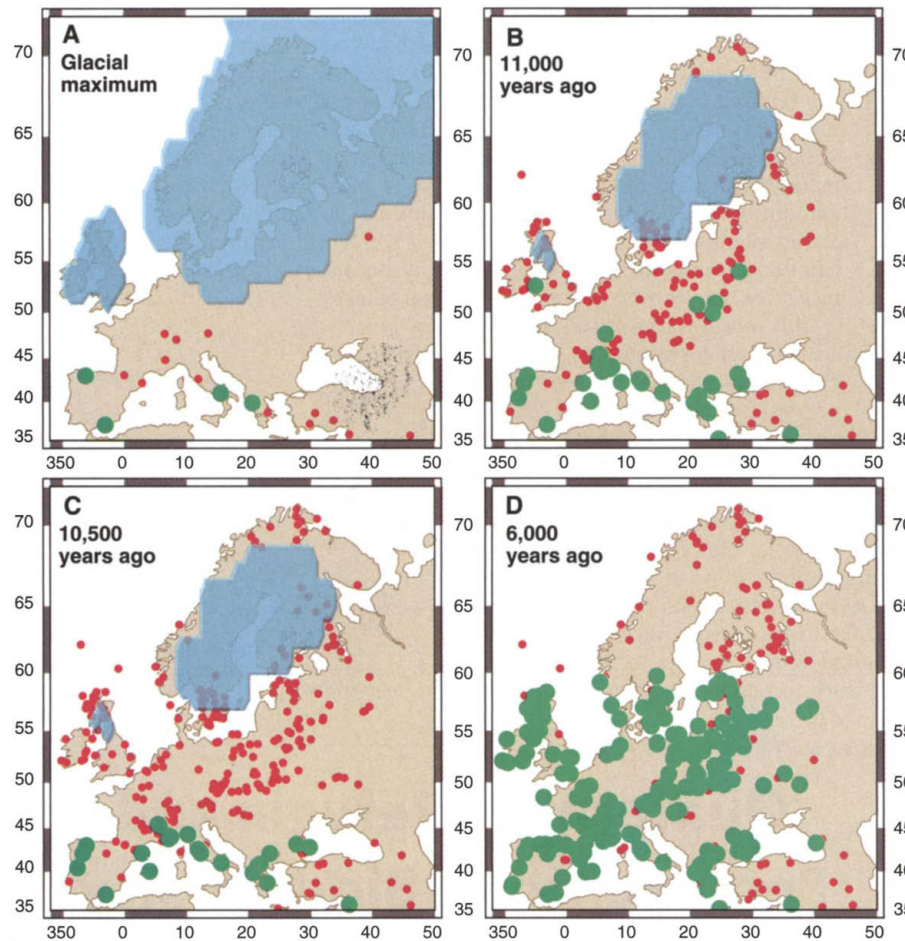
tions have dramatically affected the geographic distribution of species (5).

Assessing changes in past geographic distributions is challenging, and the few data that are available are mainly for the last glacial and the current interglacial. Range changes have been analyzed from

Such a contraction-expansion model is well documented by pollen data in Europe and northern America. European glacial refugia for many plant and animal species were likely localized in southern mountains, where varied topography results in a variety of microclimates that

iting putative refugial areas, by integrating climate model simulations, modern biogeography, past biogeography through paleodata, and genetics. However, identifying refugia and formulating predictions are challenging for many reasons. First, continuous and high-resolution paleorecords spanning at least one climatic cycle are scarce and available for only a few taxonomic groups. Second, it has been shown that each species reacted independently to Quaternary climatic changes in terms of persistence in a refugium, migration rates (9), and colonization routes (10). Therefore, generalizations should be made with extreme care. Third, what happens during one cycle might not be necessarily predictive of what will happen in the future. For example, in Europe, the hornbeam (*Carpinus betulus*) was the dominant tree species during the last interglacial, and beech (*Fagus sylvatica*) did not expand, while during the present interglacial hornbeam shows much lower densities, and beech has extensively colonized the continent. Finally the recent human influence on both biodiversity and climate further complicates any prediction.

Despite these difficulties, Quaternary refugia represent areas of special value for the long-term persistence of biodiversity. Several sophisticated computational methods have been developed to design networks of natural reserves that aimed at protecting the maximum number of species at minimum cost (11, 12). These methods, which are based on modern geographic distributions, could also take into account temporal variation in species ranges that can be estimated from paleodata. This is particularly important in the context of expected rapid climatic change related to the greenhouse effect. Applying lessons from the past might greatly improve the long-term efficiency of our conservation efforts.



Traveling species. Geographic distribution of deciduous oaks obtained from the European Pollen Database (13). During the last glacial maximum (A), ~18,000 years before the present, the deciduous oaks survived in a few refugia around the Mediterranean (green dots) and were not present elsewhere in Europe (red dots). During the postglacial period, the ice cover [blue area (14, 15) in (A) and (B)] reduced progressively, and the oak started to migrate northward (B) when a sudden cold climatic event, the Younger Dryas, which lasted about 8 to 10 centuries, constrained it to retreat southward (C). The expansion of the deciduous oaks reached its maximum extent in Europe around 6000 years ago (D).

fossil deposits such as beetle remains (6) or pollen grains (7), in an attempt to document past climatic variations and paleoenvironments. In Northern Hemisphere temperate regions, during cold periods, the geographic ranges of most species are restricted to one or a few refugia in the south. During the subsequent warming, each species expands its range, mainly northward, into available space according to its own dispersal abilities and ecological requirements. When the climate becomes cooler, northern populations may simply disappear, leaving no descendants.

provide suitable habitats during both warm and cold periods. Thus these refugia could have been important for the long-term survival of species (8). For example, if a species left a refugia during warm periods, that could lead to the complete extinction of that taxon during the next cooling.

The study of Tzedakis *et al.* (1) pinpoints one area that served as a refugium for several species. Obviously, other refugia could have existed for these and other species. This work should stimulate further interdisciplinary research aimed at delimiting

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