Every year, monarch butterflies (Danana plexippus) migrate several thousand miles between their breeding sites in eastern North America and their overwintering sites in Mexico. During the spring and summer, monarchs fly to their large breeding territory east of the Rocky Mountains and into Canada, where they lay eggs on milkweed plants (Asclepias spp.), the only food source for their caterpillars. After four generations, the butterflies fly south in late summer to overwinter in comparatively tiny high-elevation fir forests in central Mexico (1). Data released earlier this year by the World Wildlife Fund (WWF) Mexico and the North American Butterfly Association (NABA) suggest that reduced success during migration, due to environmental and anthropogenic factors, may help explain the falling monarch population (see the figure).

The decline of monarchs to dangerously low numbers in their Mexican overwintering sites, especially between 2010 and 2014, led to a petition to the U.S. Fish and Wildlife Service to list the butterflies as threatened under the Endangered Species Act. The petition is controversial (2) because monarch populations are found across the world and they are not threatened as a species. However, the sustainability of their long-distance migration in the Americas is in question, and understanding the mechanisms behind the monarch’s decline may contribute to the dwindling of this iconic butterfly’s population.
mechanisms driving their decline is crucial to reversing the trend. Monarchs have experienced a decline over decades and face diverse threats, including extreme weather, pesticides, habitat loss, and disease (table S1). The U.S. Fish and Wildlife Service is required by law to reach a decision about federal protection by June 2019.

Population dynamics of migratory animals must be understood in terms of ecological limits across the whole cycle of breeding, migration, and overwintering (3). For monarchs, this challenging task has been advanced not only by traditional academic work, but by 25 years of monitoring by nongovernmental organizations like the WWF and by large numbers of citizen scientists (table S2). This collaborative effort has provided clear evidence for a precipitous decline of monarchs during overwintering in Mexico and during their first generation in spring in the Gulf states of the southern United States (4). However, evidence of this decline diminishes during the next three summer generations as monarchs migrate to the Midwest and Northeast of the United States and into Canada (see the figure).

Agricultural intensification, particularly the widespread adoption of herbicide-tolerant crops in the Midwest, has reduced the availability of milkweed as a food source for monarch caterpillars, and this has been championed as the cause of the monarch’s decline (5). Although the number of eggs produced regionally has declined substantially in the Midwest (6), this trend is ambiguous in the Northeast and in broadscale counts of adult butterflies (4, 7). Mortality during the annual autumnal migration to Mexico has received less attention, but its potential role in the decline was implicated by studies attempting to connect the abundance of migrating butterflies in late summer to the abundance of those that arrived in Mexico (4, 8, 9).

Mortality during migration threatens other migratory animals (10) and may have increased in recent years for monarchs, potentially contributing to the declines in the overwintering population. For example, the abundance of monarchs was one of the highest in decades in the Northeast during the 2017 breeding season, but in the subsequent winter, the population was well below historic levels in Mexico. The autumn of 2017 was the hottest in over 100 years, and the extended warmth induced an extra generation of butterflies late in summer.

This delayed much of the monarch migration, potentially changing the rate of migratory success. Stress during the breeding season and migration may affect not only migratory success, but also the likelihood of overwinter survival and the subsequent northbound migration in spring. Continued degradation of the fir forests in the Monarch Butterfly Biosphere Reserve in Mexico could also explain declining numbers through reduced migratory success (11–13).

Butterfly migrants cease to rely on milkweed at the end of the summer. Instead, they depend on floral nectar from a range of plants, water to drink, and safe passage for their journey to Mexico. Thus, the connection between the summer and winter abundance, and factors that may disrupt migratory success, is critical for guiding monarch conservation (4, 8, 9).

Regardless of whether summer monarch abundance correlates with winter abundance on average, it is clear that migratory success is highly variable from one year to the next (see the figure). The latest data from 2017 are a case in point, showing no obvious correlation between summer and winter abundances. If nectar resources, landscape quality, and intact overwintering sites con-
continue to degrade, the discordance between summer and winter abundances may amplify. Contributing factors reducing the success of the monarch migration may also include sublethal effects of pesticides, road mortality, and increasing levels of disease (table S1). Planting regionally native milkweeds could buffer the monarch’s population but will not alleviate migratory mortality.

Recent evidence points to a decline beginning >45 years ago in another U.S. population of monarchs, which migrates within California (14). Such long-term and broadscale negative population trends suggest continent-wide changes that transcend single explanations such as herbicide-tolerant crops.

Modeling efforts are helping to elucidate the causes of the shrinking monarch populations (13), but as is the case for most declining species, multiple stressors likely conspire. Long-term monitoring must continue but is especially important in the southern United States and northern Mexico to estimate population sizes midmigration to and from the overwintering sites. Statistical analysis of the >25 years of monarch tagging data will likely shed light on migratory mortality and would be a boon from the hard work of citizen scientists (15). Beyond migratory mortality, latent negative effects of environmental and anthropogenic factors experienced during migration may affect overwintering itself and are in need of attention.

REFERENCES AND NOTES

SUPPLEMENTARY MATERIALS
www.sciencemag.org/content/360/6395/1294/suppl/DC1

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ANTHROPOLOGY
How did Homo sapiens evolve?
Genetic and fossil evidence challenges models of modern human evolution

By Julia Galway-Withinham and Chris Stringer

Over the past 30 years, understanding of Homo sapiens evolution has advanced greatly. Most research has supported the theory that modern humans had originated in Africa by about 200,000 years ago, but the latest findings reveal more complexity than anticipated. They confirm interbreeding between H. sapiens and other hominin species, provide evidence for H. sapiens in Morocco as early as 300,000 years ago, and reveal a seemingly incremental evolution of H. sapiens cranial shape. Although the cumulative evidence still suggests that all modern humans are descended from African H. sapiens populations that replaced local populations of archaic humans, models of modern human origins must now include substantial interactions with those populations before they went extinct. These recent findings illustrate why researchers must remain open to challenging the prevailing theories of modern human origins.

Although living humans vary in traits such as body size, shape, and skin color, they clearly belong to a single species, H. sapiens, characterized by shared features such as a narrow pelvis, a large brain housed in a globular braincase, and reduced size of the teeth and surrounding skeletal architecture. These traits distinguish modern humans from other now-extinct humans (members of the genus Homo), such as the Neandertals in western Eurasia (often classified as H. neanderthalensis) and, by inference, from the Denisovans in eastern Eurasia (a genetic sister group of Neandertals). How did H. sapiens relate to these other humans in evolutionary and taxonomic terms, and how do those relationships affect evolving theories of modern human origins?

By the 1980s, the human fossil record had grown considerably, but it was still insufficient to demonstrate whether H. sapiens had evolved from local ancestors across much of the Old World (multiregional evolution) or had originated in a single region and then dispersed from there (single origin). In 1987, a study using mitochondrial DNA from living humans (2) indicated a recent and exclusively African origin for modern humans. In the following year, one of us coauthored a review of the fossil and genetic data, expanding on that discovery and supporting a recent African origin (RAO) for our species (2).

The RAO theory posits that by 60,000 years ago, the shared features of modern humans had evolved in Africa and, via population dispersals, began to spread from there across the world. Some paleoanthropologists have resisted this single-origin view and the narrow definition of H. sapiens to exclude fossil humans such as the Neandertals (3). In subsequent decades, genetic and fossil evidence supporting the RAO theory continued to accumulate, such as in studies of the genetic diversity of African and non-African modern humans (4) and the geographic distribution of early H. sapiens fossils (5), and this model has since become dominant within mainstream paleoanthropology.

Different views on the amount of genetic and skeletal shape variation that is reasonably subsumed within a species definition directly affect developing models of human origins. For many researchers, the anatomical distinctiveness of modern humans and Neandertals has been sufficient to place them in separate species; for example, variation in traits such as cranial shape and the anatomy of the middle and inner ears are greater between Neandertals and H. sapiens than between well-recognized species of apes (6). Yet, Neandertal genome sequences and the discovery of past interbreeding between Neandertals and H. sapiens (7) provide support for their belonging to the same species.
Supplementary Materials for

Mechanisms behind the monarch’s decline

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This PDF file includes:

Materials and Methods
Supplementary Text
Tables S1 and S2
References
Materials and Methods

The population index for monarch butterflies at the highland Mexican overwintering sites is the area of forest covered by the roosting monarchs (reported in hectares by WWF-Mexico: [http://www.wwf.org.mx/?uNewsID=324152](http://www.wwf.org.mx/?uNewsID=324152)). The population index for monarch butterflies in the Northeast and Midwest summer breeding grounds were calculated from the citizen science dataset curated by North American Butterfly Association (NABA: [http://www.naba.org/](http://www.naba.org/)), updated from Inamine et al. (1). To focus on the migratory summer breeding populations, we removed counts taken west of 105°W and then subsetted the NABA counts based on their geographic coordinates to Northeast (north of 34.5°N and east of 79°W) and Midwest (north of 34.5°N and west of 79°W). A spring generation in the gulf states (most prominently in Texas) is not shown here. As in Inamine et al. (2016), within each region, we calculated a temporal moving average to smooth spatially and temporally variable sampling effort; for a given day, we calculated an equally weighted average of all the counts in the region falling in a seven-day window, centered around that day. The population index for each year was then calculated by summing the averages between 27 March and 3 October corresponding to the summer breeding season.

Supplementary Text

Index of butterfly abundance in the Midwest and Northeast is based on data from NABA. See Inamine et al. (1) for data through 2014. Relative population data shown in the main article are relative to the 10-year average for each census region (2008-2017): Midwest 10-year average = 163.1; Northeast 10-year average = 85.2; Mexico 10-year average = 2.6. The Midwest indices were 99.01 (2014), 236.33 (2015), 89.39 (2016) and 192.57 (2017). The Northeast indices were 46.37 (2014), 43.44 (2015), 28.42 (2016) and 142.36 (2017). The indices between regions are not directly comparable, but give an indication of population fluctuations when relativized against the 10-year average.
Table S1.
Threats that may be contributing to the decline of the eastern monarch butterfly annual migratory cycle, with recent references that address the issue.

<table>
<thead>
<tr>
<th>Possible threat</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest degradation at the overwintering sites, primarily due to logging,</td>
<td>(2-6)</td>
</tr>
<tr>
<td>including small scale logging in the past five years</td>
<td></td>
</tr>
<tr>
<td>Climate change, including forest changes and extreme weather events</td>
<td>(2, 7-9)</td>
</tr>
<tr>
<td>(winter freezes, drought, etc.)</td>
<td></td>
</tr>
<tr>
<td>Ecotourism at the overwintering sites (little studied, but increasing)</td>
<td>(3)</td>
</tr>
<tr>
<td>Biotic enemies of the monarch, including disease, vertebrate and</td>
<td>(6, 10, 11)</td>
</tr>
<tr>
<td>invertebrate predators, and insect parasitoids</td>
<td></td>
</tr>
<tr>
<td>Herbicides / genetically modified herbicide-tolerant crops, leading to the loss</td>
<td>(6, 12, 13)</td>
</tr>
<tr>
<td>of milkweed</td>
<td></td>
</tr>
<tr>
<td>Insecticides, including genetically modified insecticidal crops, with a recent</td>
<td>(6, 14, 15)</td>
</tr>
<tr>
<td>focus on neonicotinoids</td>
<td></td>
</tr>
<tr>
<td>Non-native plants in the Apocynaceae, including <em>Asclepias curassavica</em> and</td>
<td>(16-18)</td>
</tr>
<tr>
<td>swallowworts (<em>Vincetoxicum nigrum</em> and <em>V. rossicum</em>), that may be ecological</td>
<td></td>
</tr>
<tr>
<td>traps or disrupt the migration</td>
<td></td>
</tr>
<tr>
<td>Reduced nectar availability during the southern migration (diverse plants</td>
<td>(19, 20)</td>
</tr>
<tr>
<td>other than milkweeds, which are typically not flowering in autumn</td>
<td></td>
</tr>
<tr>
<td>Monarch mortality due to collisions with automobiles,</td>
<td>(21)</td>
</tr>
<tr>
<td>especially during the southern migration in autumn</td>
<td></td>
</tr>
<tr>
<td>Electromagnetic fields or microwave emissions which may disrupt navigation</td>
<td>(22)</td>
</tr>
<tr>
<td>during migration</td>
<td></td>
</tr>
</tbody>
</table>
Table S2.
Data commonly used to calculate monarch population size indices. Only North American Butterfly Association and World Wildlife Fund datasets are discussed in the main text. Other datasets have been used to make various arguments about the decline of eastern North American monarchs and the connectivity of the population across the annual migratory cycle. Benefits and limitations of each are outlined in the description.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Description</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>North American Butterfly Association</td>
<td>Number of butterflies recorded by citizen scientist throughout the year, with the largest samples in the Northeast and Midwest USA in the middle of summer. Volunteers may introduce biases. The data show no summer decline between 1993-2017. Denser sampling across space and time are especially needed during the fall migration in the south central USA and northern Mexico.</td>
<td>(1, 23, 24)</td>
</tr>
<tr>
<td>World Wildlife Fund – Mexico</td>
<td>Area of forest densely occupied by overwintering butterflies in the central Mexican highlands in and around the Monarch Butterfly Biosphere Reserve. Actual number of butterflies is difficult to estimate. The data show a strong decline in overwinter population size between 1993-2017. It is unclear if monarch density has changed over time and this could bias this population index.</td>
<td>(2, 25)</td>
</tr>
<tr>
<td>Cape May, NJ</td>
<td>Transect counts of migrating butterflies recorded in Cape May, NJ. Cape May is one of the funneling points where south migrating butterflies near the east coast concentrate. The data do not show a decline between 1993-2014. It has been argued that very few of these monarchs make it to Mexico, although the published data are unclear on this.</td>
<td>(26, 27)</td>
</tr>
<tr>
<td>Peninsula Point, MI</td>
<td>Transect counts of migrating butterflies recorded in Peninsula Point, MI. Peninsula Point is one of the midwestern funneling points where south migrating butterflies concentrate, especially from southern Canada. The data do not show a decline between 1996-2014.</td>
<td>(26, 28)</td>
</tr>
<tr>
<td>Long Point, Ontario</td>
<td>Counts of migrating butterflies recorded in Long Point, Ontario. Another funneling point, between Cape May and Peninsula Point, where south migrating butterflies concentrate. The data show weak evidence for a directionally changing population (including weak evidence for temporal increases and declines 1995-2014). Combining the three peninsular population estimates would be a powerful approach to understanding this critical timepoint in the annual migratory cycle (the start of the fall migration).</td>
<td>(29)</td>
</tr>
<tr>
<td>Ohio Lepidopterist Society</td>
<td>High resolution transect counts of summer butterflies recorded across 90 sites in Ohio, an important breeding area for monarchs. The data do not show summer decline between 1997-2008.</td>
<td>(31-32)</td>
</tr>
<tr>
<td>Monarch Larval Monitoring Project</td>
<td>Number of monarch eggs produced by region is calculated from number of eggs observed per stem and multiplied by an estimate of the density of milkweeds (only estimated in Iowa for several studies, with a smoothed exponential decay function of milkweed density). Extensive monarch egg and larval sampling through much of the eastern USA. A decline is observed in number of eggs produced regionally in summer. Mortality during the egg and larval stage is typically &gt;90%, introducing uncertainty to these data. Additionally, these data show decreasing survival rates of caterpillars between 1997-2014, suggesting that increasing mortality factors after oviposition may contribute to the population decline.</td>
<td>(12, 33, 34)</td>
</tr>
</tbody>
</table>
References


