Locust plagues, climate variation, and the rhythms of nature

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The ancient records of locust plagues can be traced back to the Old Testament, when locust swarms were one of the 10 plagues inflicted on the Egyptians by God according to the book of Exodus. The impact that these plagues had on agricultural societies in terms of crop damage, famine, and economic loss is so deeply rooted in the psyche of modern humans that even today the vision of a dark cloud of flying locusts disturbs us. Indeed, locust outbreaks represent an important threat in several regions of the planet, including Australia, Africa, and Asia. Because these outbreaks seem to be triggered by climatic factors such as heavy rainfalls, droughts, or floods, a key approach to the problem is to understand the interaction between climate and ecology, which represents a traditional and venerable approach among population ecologists.

Humans have been relating the year-to-year variation in climatic conditions with the abundance of hunting and fishing since the hunter-gatherer period. With the appearance of agriculture, humankind started to learn about the effects of climate on crop yields and on plague triggering. However, humans have failed to notice the long and slow drift of changes in climatic conditions, and only in the last century have we become aware of the long-term changes in climate and their ecological consequences. This problem is addressed in this issue of PNAS by Stige *et al.* (1), who analyze a unique 1,000-year time series of migratory locust outbreaks in China, combined with reconstructed data of precipitation and temperature.

Using simple statistical models, Stige *et al.* (1) show how temperature and precipitation influence migratory locust abundance at timescales between 50 and 200 years. Although at the annual scale temperature shows positive effects on locust dynamics (1), the authors observe a negative association between temperature and locust abundance at a multidecadal scale. In addition, Stige *et al.* report the statistical association among locust abundance, frequencies of floods and droughts, and temperature and precipitation records during the last 1,000 years in the Yangtze delta. The interesting finding is that the three phenomena are highly correlated: Locust outbreaks are statistically associated with cold and wet periods, and they are more frequent during decades characterized by a high frequency of floods and droughts. In addition, higher frequencies of droughts and floods occur during cold and wet periods.

Factors Driving Fluctuations May Not Predict Long-Term Responses of Natural Populations

How can we reconcile these results with the positive effects of temperature on the year-to-year locust dynamics? The explanation of this apparent contradiction lies in the different dynamic processes being observed at different timescales. At the annual timescale, locust dynamics are positively correlated to temperature because of the direct effects of the latter on insect development, reproduction, and survival (2). These year-to-year fluctuations, which represent the basic ecological phenomenon that population dynamicists try to understand and predict (3–5), are mostly due to mortality and birth rates, and define how the fitness of an average individual changes under different ecological factors (density, food, enemies, and climate) (4).

> **Locust outbreaks represent an important threat in several regions of the planet.**

Stige *et al.* (1) provide unique results that place population dynamic analyses into a different perspective: What factors drive the long-term dynamics of natural populations? The locust outbreak time series reflects a set of ecological processes different from those occurring from year to year. The results show the slow changes in time and space that populations experience through generations as well as the ecological processes that can seldom be observed in a lifetime. The hypothesis proposed by Stige *et al.* is that the negative association between temperature and locust dynamics at the decadal and regional scales reflects the dynamics of suitable breeding habitats and not the local fluctuations driven by birth and mortality rates. The lessons and implications of this finding are clear: Predicting the long-term ecological consequences of climate change can be extremely difficult when population models derived from short-term dynamics are used, because the factors driving the long-term dynamics of natural populations can be completely different from the factors determining year-to-year variability.

Population ecologists are becoming aware of the importance of multidecadal patterns of climatic variation for understanding population changes in the long term (6). The processes underlying this low-frequency variability are related to regime shifts (7) and large-scale changes in vegetation and productivity patterns (8); the resulting implication for population ecologists is that factors limiting natural populations will change and shift from time to time in a multidecadal or century timescale. Although the importance of shifting limiting factors in time has been previously addressed on theoretical grounds (4), few empirical studies have focused on this problem. The study by Stige *et al.* (1) is particularly enlightening in this regard. In fact, the analysis of the 1,000-year dynamics of locust outbreaks points out that population dynamicists need to consider this low-frequency variability to predict the long-term fate of natural populations. Year-to-year fluctuations in natural populations are frequently caused by a few factors, with overwhelming evidence that population dynamics are low-dimensional and simple (9), but complexity can arise when limiting factors change from time to time at a very low-frequency variability, such as the variability Stige *et al.* show for locust abundance.

Population Dynamics Complexity May Be Related to the Shifting of Limiting Factors in Time

The oscillations of animal populations have fascinated ecologists since the

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study by Elton (10), who was intrigued by the possibility of finding a causal connection between fluctuations in the number of animals and climatic variability. After decades of debate about the factors determining interannual population fluctuations, most ecologists now agree about the roles of both endogenous and exogenous (climatic) forces (11). However, we cannot accurately predict long-term trends in climate and their ecological consequences, a key problem to solve if we wish to explore sustainability or predict the consequences of climate change. The article by Stige *et al.* (1) addresses this central problem.

More than 30 years ago, in *Children of Dune* (12), Frank Herbert wrote about the problem of long-term effects of climate change, and I think that his words reflect the essence of the contribution by Stige *et al.*: "Lonely, finite humans may observe climatic provinces, fluctuations of annual weather and, occasionally observe such things as 'This is a colder year than I've ever known.' . . . But humans are seldom alerted to the shifting average through a great span of years. And it is precisely in this alerting that humans learn how survive on any planet. They must learn climate."

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