for two-dimensional electron gas with a Rashba-type spin-orbit interaction produced by the asymmetry of the potential. The intrinsic SHE is a result of the inherent property of the material, as opposed to the extrinsic SHE caused by scattering.

Elucidating the nature of the pure SHE is now an emergent issue for experimentalists as well as theorists. Despite the difficulties associated with the absence of the Hall voltage in the pure SHE, two groups have succeeded in measuring the spin accumulation in nonmagnetic semiconductors by optically detecting the spin accumulation at the sample edge. Kato *et al.* (*16*) spatially resolved the Kerr rotation of the reflected light from n-type bulk GaAs and InGaAs samples and found accumulation of opposite sign at the two edges of the sample. Subsequently, Wunderlich *et al.* (*17*) measured the polarization of light emitted from a p-n junction placed at the edge of a structure. Kato *et al.* suggested that the observed effect may be the extrinsic SHE, as the spin Hall conductivity is low and independent of the crystal orientation, whereas Wunderlich *et al.* concluded that the effect is the intrinsic SHE, because the magnitude of the polarization is consistent with the theoretical prediction. The interpretation of the experimental results is complex, because the current theories predict that the intrinsic SHE is suppressed by disorder effects for two-dimensional electron gas with a Rashba type spin-orbit interaction (*18*), whereas it can remain finite, depending on the type of the spin-orbit interaction (*19*) and the electronic states. The latter prediction may explain the experimental results within the framework of the intrinsic SHE. On the other hand, a recent theory on the extrinsic effect predicts the observed SHE within experimental error with no adjustable parameters (*20*). Nonconservation of spin in the presence of the spin-orbit interaction is also a source of difficulty associated with theoretical analysis.

Very recently, Sih *et al.* have imaged the SHE in a series of two-dimensional electron gases within (110) AlGaAs quantum wells having the crystal orientation in which the Dresselhaus and Rashba spin-orbit interactions are separated (the former out-of-plane, the latter in-plane) (*21*). This information will aid us in establishing the microscopic relation between the spin Hall current and the observed quantities. On the theoretical front, SHE in insulators and its quantized version has been proposed (*22*–*24*); a search for material systems that allow observation of such an effect has been initiated.

The SHE has a practical relevance to the field of spintronics, where spin polarization, manipulation, and detection are essential. Theoretical studies to link SHE with measurable quantities such as spin accumulation and an optical signature are highly desired, because even if spin Hall current itself is intrinsic, the stationary spin accumulation is a result of a balance between spin Hall current and intrinsic/extrinsic effects of the spin relaxation at the edges of the sample. Further systematic experiments that use controllable parameters such as doping or gate voltage certainly will provide us a clear view of SHE. A unified picture of the Hall effect is still being developed 126 years after its discovery.

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ECOLOGY

Making Sense of Evolution in an Uncertain World

Vincent A. A. Jansen and Michael P. H. Stumpf

Many organisms have adapted to a life with uncertainties. For instance, some pathogenic bacteria have genes that can be switched off to stop disease progression in a host organism or prevent their recognition by an immune system. Such strategies increase an organism's reproductive success and tend to be found in environments in which the conditions are strongly fluctuating. To understand the development of such strategies, evolutionary biologists determine the long-run reproductive success of organisms in fluctuating environments by calculating the Lyapunov exponent, a measure of the average exponential growth rate in an unpredictable environment. Often these calculations are ferociously difficult and rarely lead to simple results. On page 2075 of this issue, Kussell and Leibler (*1*) describe a new method to approximate the long-term reproductive success in fluctuating environments and reveal remarkable insights into evolution in an uncertain world.

Consider again bacteria, which have developed strategies to cope with a sea of potential troubles in their rapidly changing environments, such as the variable natures of their hosts or the changing number of available hosts. Many pathogenic bacteria have evolved phase variation, a process that turns the expression of certain genes on and off (*2*, *3*). This "switch" works through genetic reorganization, mutation, or modification of the regions in the bacterial genome that control gene expression. These genetic changes are heritable, reversible, and stochastic. The effect is that a single bacterium within a population switches independently of others, and the progeny of a bacterial population is phenotypically diverse. This phenotypic diversity serves as a buffer against fluctuations in the environment and allows the population to adapt to unpredictably changing environments.

This strategy of randomization of phenotype is known to ecologists as bet-hedging (*4*). Bet-hedging does more than just produce variation that reduces the chances of population extinction: In a fluctuating environment, bet-hedging evolves and bet-hedgers will in the long run replace equally diverse populations whose members have offspring that are all the same. Even if this

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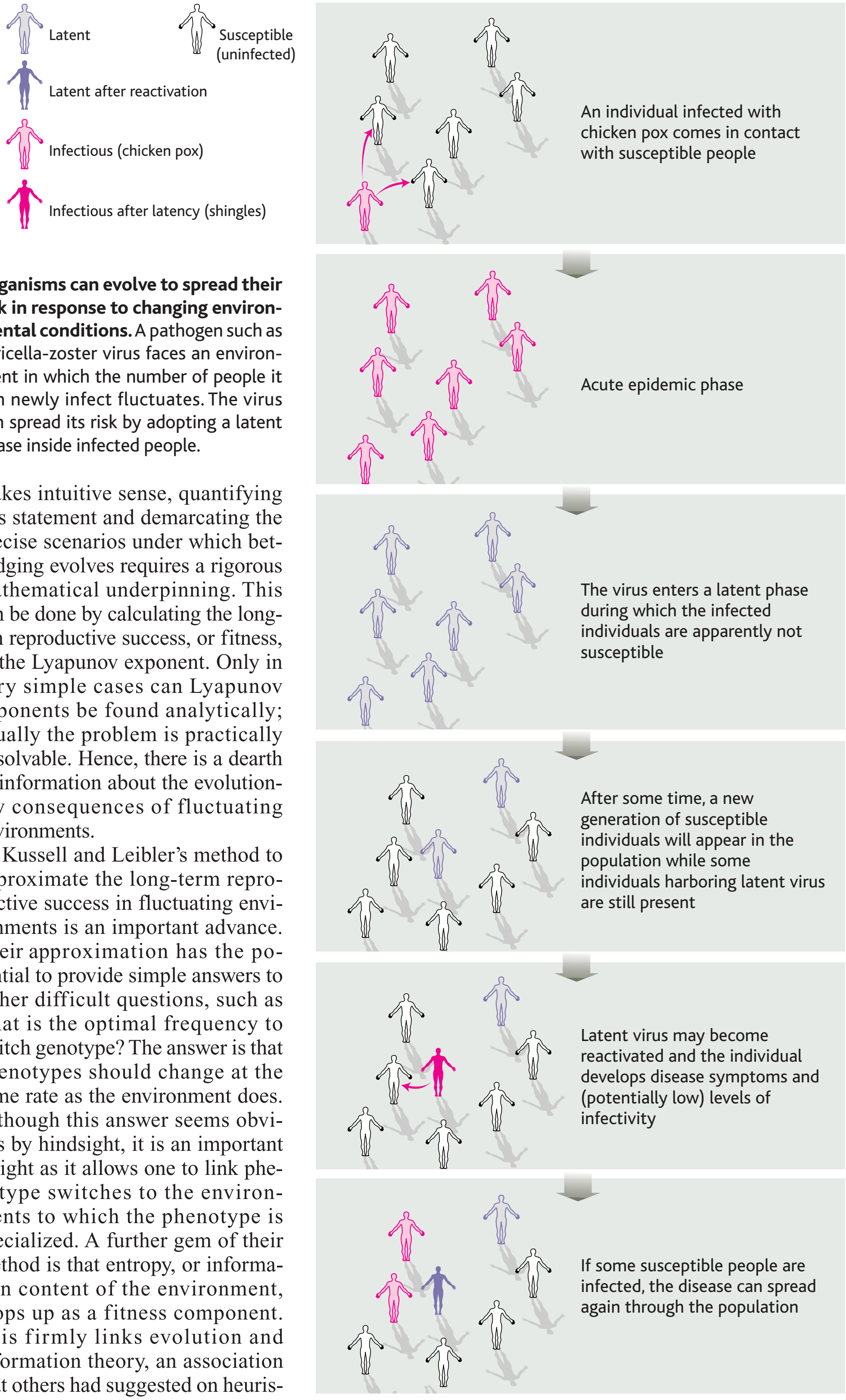

Organisms can evolve to spread their risk in response to changing environmental conditions. A pathogen such as varicella-zoster virus faces an environment in which the number of people it can newly infect fluctuates. The virus can spread its risk by adopting a latent phase inside infected people.

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makes intuitive sense, quantifying this statement and demarcating the precise scenarios under which bet-hedging evolves requires a rigorous mathematical underpinning. This can be done by calculating the long-run reproductive success, or fitness, as the Lyapunov exponent. Only in very simple cases can Lyapunov exponents be found analytically; usually the problem is practically unsolvable. Hence, there is a dearth of information about the evolutionary consequences of fluctuating environments.

Kussell and Leibler's method to approximate the long-term reproductive success in fluctuating environments is an important advance. Their approximation has the potential to provide simple answers to rather difficult questions, such as what is the optimal frequency to switch genotype? The answer is that phenotypes should change at the same rate as the environment does. Although this answer seems obvious by hindsight, it is an important insight as it allows one to link phenotype switches to the environments to which the phenotype is specialized. A further gem of their method is that entropy, or information content of the environment, crops up as a fitness component. This firmly links evolution and information theory, an association that others had suggested on heuristic grounds (*5*).

The main question addressed by Kussell and Leibler is whether it is evolutionarily favorable for an organism to monitor the environment to optimize its response. The authors do this by contrasting two different ways of producing variable offspring: either by chance and irrespective of the environmental conditions (stochastic phenotype switching) or by giving rise to offspring with a suitable phenotype after sensing a change in the environment (responsive switching). Which of the two strategies has the highest reproductive success? The real surprise of this paper is that in many cases stochastic switching will be selected over sensing and response. Because the environment has to be monitored, continuous responsive sensing is costly as it requires energy expenditure and the maintenance of suitable molecular machinery, particularly if environmental changes occur infrequently. Stochastic switching also carries a cost, in that it produces individuals that are maladapted to their environment, but this turns into an advantage if the environment changes and these individuals become a standing army from which the most suitable recruits are selected to deal with the new conditions. If this cost is smaller than the cost of continuously sensing the environment, the stochastic switching strategy is selected over responsive switching.

This carries the implication that simple stochastic mechanisms of phase variation abound, not because organisms are constrained in the development of a sensing mechanism, but because this simple stochastic switching mechanism is selectively superior. These insights have some intriguing consequences for the study of the mechanisms of pathogenicity. For instance, the varicella-zoster virus causes chicken pox as a primary infection (see the figure). However, the virus can switch off the expression of many of its genes and "go into hiding" in neuronal cells. After many years, it can reemerge in the form of shingles. Contact with a person with shingles can lead to chicken pox in someone who has never had chicken pox and has not received the varicella vaccine. It is not known why the virus reactivates, and much effort has been devoted to unraveling the reactivation mechanism (*6*). It has been postulated that the latency of varicella-zoster virus is a bet-hedging mechanism in response to the fluctuating number of susceptible individuals in the local population (*7*). Kussell and Leibler's result illustrates why there might not be a refined trigger mechanism: For a virus in a latent state, it must be costly, if not impossible, to continually monitor or sense the number of susceptible individuals surrounding the carrier. If so, a simple stochastic switch is much

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more effective than a sophisticated sensing mechanism.

The ability to analyze long-term outcomes of evolutionary processes in stochastically fluctuating environments is of fundamental importance for understanding evolutionary biology and can, in particular, contribute important insights into the biology of pathogens. As it turns out, randomly creating phenotypic diversity—or not putting all your eggs into one basket—may be all that is necessary, and the work by Kussell and Leibler allows us to assess when this is the case.

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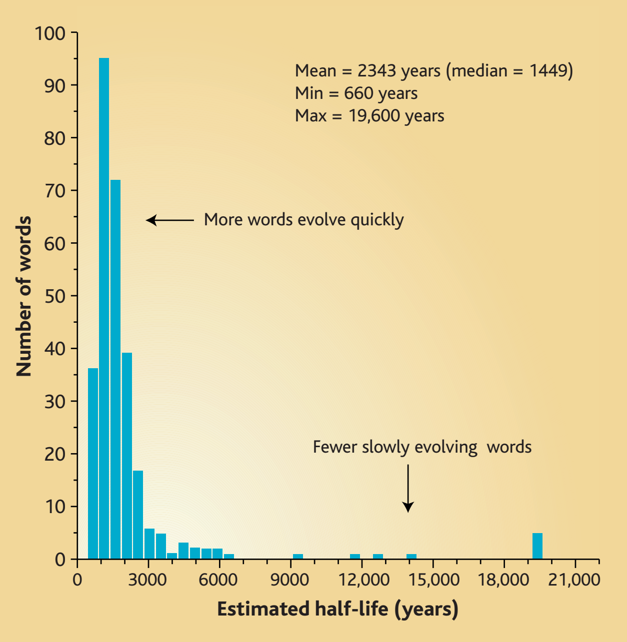
EVOLUTION

Pushing the Time Barrier in the Quest for Language Roots

Russell Gray

Questions about human origins have an enduring fascination. For centuries, scholars and laypeople have wondered where groups such as Polynesians or Indo-Europeans came from. Linguistic evidence plays a vital role in tracking the movement of people by leaving linguistic trails that are analogous to the genetic signatures that molecular biologists study. Early European explorers in the Pacific, for example, were struck by the remarkable similarities between the far-flung languages of the Pacific (the word for hand in Hawaiian and Samoan is *lima*, in Marquesan it is *'ima*, and in Tahitian *rima*). It might seem a simple matter, therefore, to trace the origin of words used in linguistic and cultural groups and thereby unravel connections between the peoples of the world that extend deep in the past. Perhaps it might even be possible to infer the initial "mother tongue" spoken before our languages diverged. Alas, the task for historical linguists and prehistorians is not this easy. First, superficial similarities in vocabulary must be separated from genuine similarities due to descent. Linguists call these genuine homologies "cognates." The diagnosis of cognates is a challenging task that requires detailed specialist knowledge to detect systematic sound correspondences. Then an even more difficult problem is encountered: The rate of vocabulary evolution is so rapid that it erases distant or "deep" historical connections.

Consider the following thought experiment: Imagine that two languages each diverge in their basic vocabulary from a common ancestor at roughly 20% every thousand years (this is a rough but not entirely arbitrary figure). After 1000 years, 64% of the languages' basic vocabulary would be cognate; after 2000 years, 41%; and after 10,000 years, just over 1%. The problem of rapid lexical decay is exacerbated by chance similarities and recent borrowings that obscure this weak historical link or "signal" (for example, the Maori and Modern Greek words for eye, *mata* and *mati*, superficially appear similar, but no one seriously postulates that this reflects some deep historical link). Instead, most linguists believe that after about 8000 to 10,000 years it is impossible to differentiate between homology and chance resemblances or borrowings. They are therefore highly skeptical of arguments for ancient language relationships, especially when cognacy judgments are made with less than the normal standard of rigor. One highly controversial example is Ruhlen's claim (*1*) that words ostensibly related to a Proto-Amerind term **t'ana* (child, sibling) provide evidence for a putative 12,000-year-old Amerind language family. As Campbell (*2*) has pointed out, the semantic variation that Ruhlen allowed (meanings including small, woman, cousin, son-in-law, old man, friend, and some 15 other terms), coupled with relatively loose phonetic matches (Ruhlen treats *tsuh-ki* and *u-tse-kwa* as related to **t'ana*), make chance resemblance highly likely.



The rate of vocabulary change. A word's half-life is the amount of time required for there to be a 50% chance that it will be replaced by a new word. Most words have a half-life of 2000 years. However, a small number of words have a half-life greater than 10,000 years. This shows that despite the fast average pace of language evolution, some meanings, like highly conserved genes, evolve at a slow rate [adapted from (*3*)]. The *y* axis is the number out of a sample of 200 meanings.

Recent work by Pagel (*3*) suggests that the prospects for discovering deep links between languages may not be quite so bleak. The calculations above assumed that all words change at the same rate. This is not realistic. Pagel adapted stochastic models of genetic evolution to the problem of lexical change. He showed that a distribution of word rates is a much better fit to the data than a single rate. This distribution has a long tail, implying that in principle there are some very slowly evolving words that remain cognate even after 20,000 years (see the figure). It is these very stable words that proponents of long-distance language relationships have focused on. However, the practical task of convincingly separating deep homologies from chance corre-

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