IS EVOLUTION
CONTINGENT OR PREDICTABLE?

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It is always a good idea, on occasion, to ask whether one's science is as good as it can be. Are my ideas novel and pushing back the frontiers of knowledge? Or am I running with the pack and following the lead of others? Am I more concerned about advancing science than fashion? Where do my abilities allow me to make the greatest contributions? What are the most promising and productive directions for ecology and evolution?

Yet some scholars see little value in forecasting the future because those forecasts are invariably wrong. Science, they argue metaphorically, is as unpredictable as the numerous intertwining branches of a wild vine. This statement reveals more about attitude than it does about the growth strategies of vines. Different species of vines compete with other plants for sunlight by growing directly toward light (phototropism), away from it (a response aptly coined apheliotropism by Darwin (1880)), or perhaps paradoxically by growing toward darkness (skototropism, Strong and Ray, 1975). So when Leon Blaustein and Burt Kotler asked me to put together this series of commemorative Darwinian essays on the future of ecology and evolution I sought, with Leon and Burt's help, a group of evolutionary and ecological thinkers whose perspectives vary, but who share the same end game to seek deeper understanding of ecology and evolution in all their varied shades and hues. I hope that at least some of their ideas will help carry us toward our shared future.

Read any text on evolution and you are bound to encounter statements in which adaptation, lacking foresight, is contingent on history. Stochastic processes limit our ability to foresee the variance on which adaptation operates, or the exact environments (and their sequence) in which it takes place. Additional problems include the absence of simple rules linking genotypes and phenotypes, variation in the connection between phenotypes and reproductive success, and the complexities of antagonistic selection (Bell, 2008). Although these facts are undeniably true, they should also discomfort anyone who thinks that evolutionary biology is a mature, predictive science.

There is a corollary. If we cannot predict the most profitable future directions for research, can we at least predict which approaches are less effective than others? Do we really need, for example, more case studies of adaptation, no matter how elegant or

For more information about the photo, see cover caption on the Table of Contents page.

novel (and no matter how newsworthy journalists may make them appear)? Should we continue to be surprised by more evidence of how rapidly adaptation can alter phenotype distributions in wild populations (how many plant and animal breeders would be surprised that directed selection causes rapid evolutionary change)? Should we continue to debate how best to estimate fitness, and then attempt to do it? Or should we consider fitness a necessary abstraction that we use to understand adaptation, then use that knowledge to explore and predict the persistence and elimination of alternative evolutionary strategies?

Every naturalist can recite example after example of convergent evolution and converging strategies. Independent evolution in similar environments produces repeated, albeit nonidentical, patterns of adaptation. The traits of gerbils and drought-adapted shrubs that define evolutionary success in Israel's deserts arose independently from those of the kangaroo rats and xerophytes in the Americas. But the strategies are similar. Bipedal locomotion enables seed-eating rodents to move quickly across risky open places and hyper-efficient kidneys allow them to thrive in the absence of free water. Small, fleshy leaves on desert plants reduce water loss. Thorns and spines help to shield other tissues from intense solar radiation. Deep, expansive root systems protect them from drought.

So although it is impossible to predict the exact course of evolution, or to anticipate how specific genetic changes will influence phenotypes, their function and fitness (emerging technologies are likely to make this possible for simple phenotypic traits), it should nevertheless be possible to project how strategies influencing fitness should evolve (Mitchell and Valone, 1990; Brown, 2001; Vincent and Brown, 2005). Can we develop effective methods whereby our study organisms reveal their adaptive landscapes, then project those landscapes onto changed (and stochastic—see Smallegange and Couslon (2009) elsewhere in this issue) environments? If so, would we not be able to forecast future evolutionary change?

How, you might ask, can we reveal adaptive landscapes without measuring fitness? The solution lies in the nature of adaptation, our conviction of its importance, and our willingness to endure criticism when we ascribe fitness, without a direct estimate, to phenotypes. Individuals should behave adaptively (Grafen, 1984). Adaptive behavior reflects phenotypic and state-dependent differences. Large male giraffes intimidate smaller rivals (Simmons and Scheepers, 1996). Small male dung beetles avoid direct confrontation with large males and secure their inheritance through stealth and deception (Moczek and Emlen, 2000). Sated foragers accept less risk than hungry ones, and starving foragers will accept any risk in order to secure food (Brown et al., 1997; Houston and McNamara, 1999; Brown and Kotler, 2004). Animals living at low density occupy different habitats than they do at high density (Fretwell and Lucas, 1969; Rosenzweig, 1981; Morris, 1988).

In each of these cases, individuals possess alternative courses of action that depend on circumstance that we can manipulate. Small males lacking any opportunities for sneaky copulations might choose confrontation over subjugation and stealth. Foragers with limited opportunities to feed in safe places may choose different strategies than do

foragers provided with safe refuges. Habitat selectors exposed to enriched habitats or competing species may alter the pattern of habitat occupancy that they use in poorer, or less diverse, environments. With appropriate experiments we can use the choices of individuals, and correlates of their success, to map their true preference and its consequences. Do males forced to confront rivals experience reduced mating success when returned to their "control population"? Do foragers given access to refuges feed more efficiently than those living with constant risk? Does their foraging behavior change when the treatments are reversed? Does an individual's habitat preference change with productivity?

If we can answer these sorts of questions, then we should be able to anticipate how different sorts of environmental changes will influence the future course of a strategy's evolution. If environmental change reduces opportunities for stealthy mating, and if small males lose in competition with large rivals, then the frequency of small males should decline. If safety is increased in risky environments, adaptations for less reckless foraging strategies will evolve. If climate change makes some habitats more productive than others, and if those habitats are preferred, then habitat preference itself should change.

Robert Holt's Soapbox (2009) starts our journey by revisiting Darwin's famous and superbly crafted closing "poem" in the *Origin*. Bob focuses our attention on the actions of insects and worms, and on the central theme "there is no life without movement". He makes the point with reference to a childhood favorite reading, *Flatland* (Abbott, 1884). He develops, in the Holtian fashion that many of us adore, a simple model of life in "Lineland" with a deceptively simple and profound message. Linearly growing populations increase their numbers according to an arithmetic progression. Life is similarly constrained in "Flatland" and "Spaceland". Neither can produce, on its own, Malthus' model of geometrically growing populations.

Isabel Smallegange and Tim Coulson (2009) challenge us to explore more fully the consequences of variation in birth and death rates. Smallegange and Coulson provide examples of new insights gained by the methods of stochastic demography and sound a clarion call for their wide application in laboratory experiments These experiments may help us gain a deeper understanding of evolution in changing environments, guide us toward new theories of density- and frequency-dependence, and modify our perspectives on evolutionary fitness. But Smallegange and Coulson also allude to an enduring problem stated forcibly by Gordon Orians nearly half a century ago (Orians, 1962), that ecological understanding is impossible without keeping natural selection "firmly in mind".

Alan Templeton (2009) leads us on Orians' quest to fully appreciate adaptation with a wonderful review of natural selection in the past, present, and future. Templeton summarizes errors in Darwin's assumptions about inheritance and problems associated with an over-emphasis on the fitness of individual organisms. But he reminds us that, in these exciting times of merging genetics with development and the ecology of individuals, Darwin's interpretations endure because he understood, at a profound level, that adaptation emerges through the interaction of inherited traits with their environment.

Adaptation is, of course, extraordinarily difficult to study, and especially so at the

spatial scales corresponding to many populations. Fortunately, landscapes exist where environmental variation is compressed to scales on the order of the movements of individual animals. Eviatar Nevo (2009) tells us how to use these wonderful "evolutionary canyons" as extraordinary natural laboratories in which to study evolutionary dynamics (Nevo, 2009). His remarkable success at gaining insight into numerous evolutionary processes bodes well for others who wish to follow his lead.

But read on and find a warning from Mark Rees, Jessica Metcalf, and Dylan Childs (2009). "Darwinian demons" lurk in the dark statistical recesses of many attempts to study selection in the wild. The assumptions of statistical models may not jive with those of evolutionary biology. In the simplest example, negatively correlated traits that influence fitness cancel one another's effect. The unsuspecting evolutionary statistician who is unaware of the trade-off will conclude, incorrectly, that neither is related to fitness. Rees et al. (2009) show us how to exorcize the demons by building more rigorous and fully parameterized models. The key feature is to recognize that "fitness is a property of the design", not of the individual. The difference forces us to pay attention to the panoply of traits and interactions that influence fitness.

The Rees et al. (2009) solution compels us to more fully describe fitness, and converges with that of Vincent and Brown's (2005) G-functions. Each requires an explicit statement about the relationship between fitness and strategies. The G-function, and related approaches of adaptive dynamics (Metz et al., 1996), allow us to contrast competing strategies in time and space, and to winnow out the losers. But their success at doing so depends on our ability to identify strategies and their relationships with fitness. The methods proposed by Rees et al. (2009) may provide a powerful way to test those insights.

This short collection of thoughtful essays portends a treasure-trove of new ideas and perspectives awaiting discovery by theory, experiment, and example. As we further explore the rich interface between evolution and ecology, recall Bob Holt's message. Exponential growth that underlies Darwin's interpretation of the "struggle for existence" applies only in worlds with movement.

So too, in a sense, does the advance of knowledge. We make progress only by developing new ways of thinking, by inventing novel solutions to persistent questions, and hopefully answering a few new ones along the way. Movement in the field of knowledge is seldom easy, but far outweighs the alternative of being stuck, as too many are, in "Pointland" where they visit and revisit the same stagnant ideas over and over again. Embrace novelty, cheer for the unexpected, and relish the thought of risky, bold, moves into the unknown.

Time will tell whether the directions hinted at here will help us explore new frontiers of evolutionary understanding. And only the passing of time will tell us how willing others might be to test their scientific mettle against the phenotypic gambit (Grafen, 1984). Perhaps, if we had more opportunities for provocative scientific journalism, more alternative editorial policies, and a deeper appreciation of ideas that truly alter our worldview, then we would be able to manipulate the behavior of scientists to assess whether pursuit of a predictive evolutionary biology is adaptive.

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