Natural Selection Fails to Optimize Mutation Rates for Long-Term Adaptation on Rugged Fitness Landscapes[*]

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Abstract

The rate of mutation is central to evolution. Mutations are required for adaptation, yet most mutations with phenotypic effects are deleterious. As a consequence, the mutation rate that maximizes adaptation will be some intermediate value. This abstract summarizes a previous publication in which we used Avida, a well-studied artificial life platform, to investigate the ability of natural selection to adjust and optimize mutation rates. Our initial experiments occurred in a previously studied environment with a complex fitness landscape (Lenski et al. Nature, 423, 2003) where Avidians were rewarded for performing any of nine logic tasks. We assessed the optimal mutation rate by empirically determining which unchanging mutation rate produced the highest rate of adaptation. Then, we allowed mutation rates to evolve and we evaluated their proximity to the optimum. Although we chose conditions favorable for mutation rate optimization (asexual organisms not yet adapted to a new environment), the evolved rates were invariably far below the optimum across a wide range of experimental parameter settings (Fig. 1). We hypothesized that the reason mutation rates evolved to be suboptimal was the ruggedness of fitness landscapes. To test this hypothesis, we created a simplified 'counting ones' (a.k.a. 'onemax') landscape without any fitness valleys and found that, in such conditions, populations evolved near-optimal mutation rates (Fig. 2, top row). In contrast, once moderate fitness valleys were added to this simple landscape, the ability of evolving populations to find the optimal mutation rate was lost (Fig. 2, bottom two rows). Additional experiments revealed that lowering the rate at which mutation rates evolved did not preclude the evolution of suboptimal mutation rates (see original manuscript). We conclude that rugged fitness landscapes can prevent the evolution of mutation rates that are optimal for long-term adaptation because of the short-term costs of traversing fitness valleys. This finding has important implications for evolutionary research in both biological and computational realms.
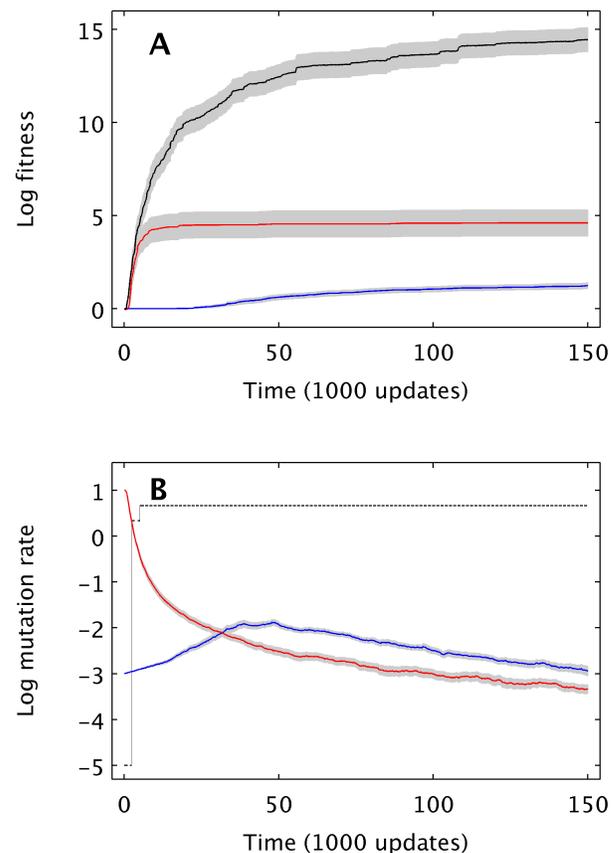
Figure 1: Evolutionary trajectories for fitness and mutation rate on a complex fitness landscape reveal that evolved mutation rates are lower and produce less adaptation (lower fitness values) than a certain (long-term optimal) non-evolving rate. (A) Evolution of average (over 50 runs) log-fitness ± 1 s.e.m. for treatments with the genomic mutation rate fixed at the empirically determined optimum rate $U_{opt} = 4.641$ (black) and for treatments with variable, evolving genomic mutation rates starting at either 10 (red) or 10^{-3} (blue). (B) Evolution of average log genomic mutation rate ± 1 s.e.m. for treatments with variable, evolving mutation rates starting at either 10 (red) or 10^{-3} (blue). The black line indicates the mutation rate that had produced the highest average fitness for that time point.
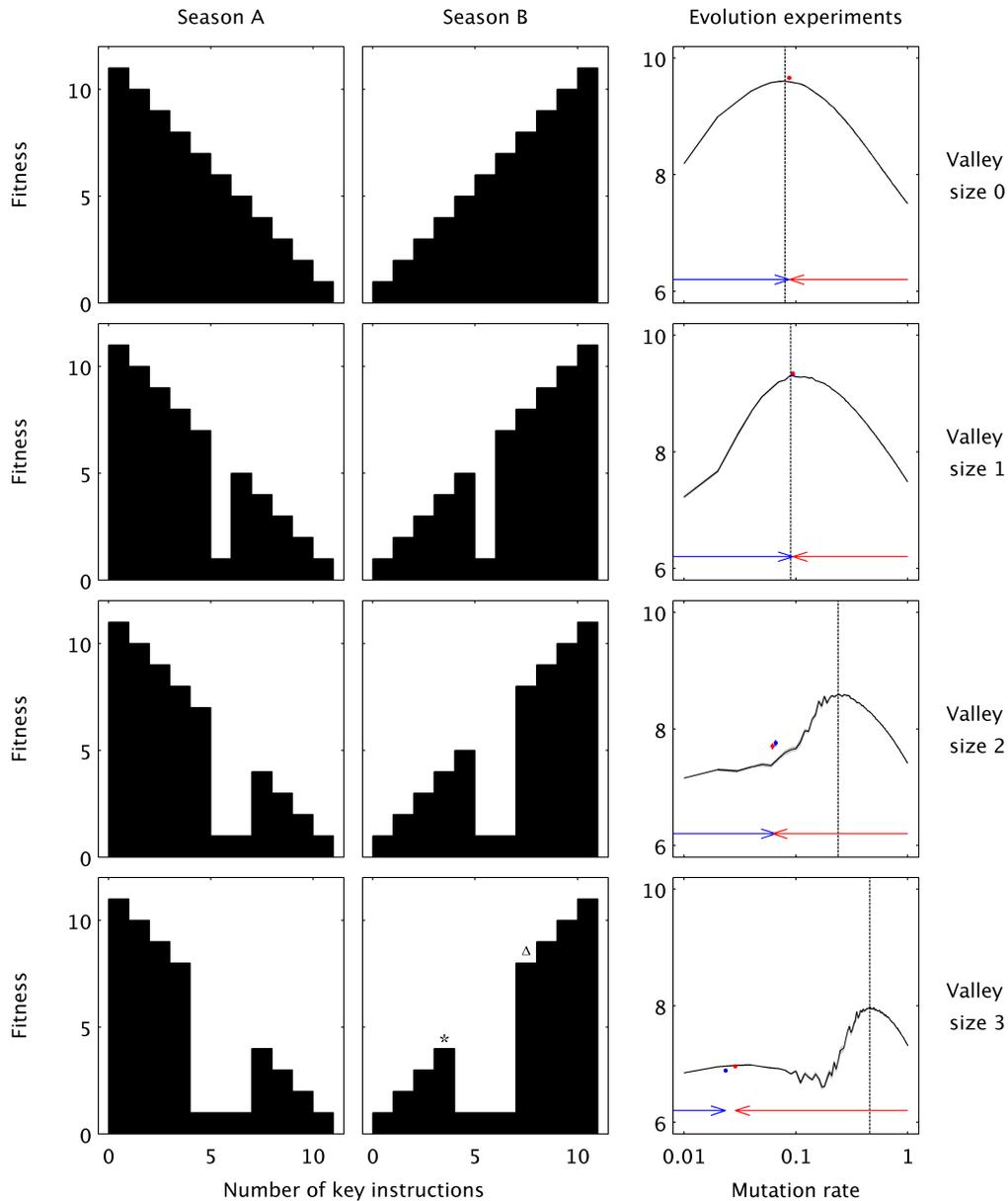
Figure 2: Evolution of mutation rates on simple fitness landscapes with different ruggedness. Here, fitness depended solely on the match between the environment and the number of a key instruction that organisms had in their genomes. In season A (left column) the key instruction was deleterious while it was beneficial in season B (center column). Rugged fitness landscapes with maladaptive valleys (rows 2-4) were introduced by setting the fitness of organisms with intermediate numbers of the key instruction to the minimum fitness level of one. The right-most column shows the results of evolution experiments under each of these selective regimes. Final fitness is shown as a function of genomic mutation rate for both static and dynamic mutation rates. The solid black line represents the average of the mean fitness across 10 runs for each of 100 different static mutation rates ranging from $U = 0.01$ to 1 in increments of 0.01. The two colored points represent the mean fitness and mutation rate, both averaged over 50 runs where the mutation rate freely evolved, with initial rates of $U = 1$ (red) or 10^{-5} (blue). Mutation rate and fitness values were time-averaged over the last 10 of 50 environmental changes. Owing to very similar final values, despite the very large initial differences, the individual colored points are indistinguishable in the first two rows, and error bars are not visible. The arrows indicate where mutation rates began and ended, on average, for the dynamic-rate experiments. Although the optimal mutation rate increases as a function of valley size (note the right-shift in the dashed line from top to bottom), the evolved mutation rates in fact decrease as a function of valley size (note the left-shift of the blue and red points from top to bottom).