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## "An Evolutionary No Man's Land" and "Reply from L. G. Harshman and A. A. Hoffmann"

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## An Evolutionary No Man's Land

The gap between evolutionary studies in laboratory versus natural populations is a persistent problem.<sup>1,2</sup> In an attempt to bridge this gap, some researchers in the early 1980s studied the quantitative genetics of laboratory populations recently founded from the wild, with and without inbreeding.<sup>3,4</sup> The dangers of such approaches were soon demonstrated experimentally.<sup>5,6</sup> Inbreeding depression and genotype-by-environment interactions make such studies unreliable guides to the evolution of populations long-established in any environment. This conclusion is reiterated to some extent in Harshman and Hoffmann's recent *TREE* perspective,<sup>2</sup> where the authors state that "The nature of laboratory selection regimes is unnatural." But, they then go on to propose complementing selection experiments in long-established laboratory populations with selection experiments in recently introduced ones. It is not clear how one could disentangle the causes of possible differences from the results of such disparate studies. Furthermore, from first principles and extant experimental studies, we expect a conflation of evolutionary effects in the recently introduced populations because of adaptation to the laboratory environment, and because of genetic and evolutionary disequilibrium. In particular, interactions between adaptation to the general laboratory environment and any particular selective regime under study could be a source of unresolvable evolutionary outcomes, as we will now explain.

Two evolutionary processes are at work in the transition from the wild to the laboratory. First, placing a population in a novel environment can cause a change in genetic variances and covariances between traits, as a result of genotype-by-environment interactions. Second, continued maintenance in this novel environment might bring about evolutionary change, perhaps because of new selection pressures or changes in breeding structure. A recently founded laboratory population will thus be in a "no man's land." We cannot use it to provide information about the original wild population, nor can we test evolutionary models that rely on the assumption that the newly transplanted population is near genetic or selective equilibrium. Surprisingly, like Harshman and Hoffmann, several recent studies have essentially repeated these mistakes.<sup>7-9</sup>

Let us conclude with an example. The empirical challenge posed by the transition from wild to laboratory conditions led us to study the evolution of a newly founded laboratory population of *Drosophila subobscura*.<sup>10</sup> We found that adaptation to the novel, laboratory environment occurred at a relatively fast rate. As an illustration, fecundity around the age of reproduction increased steadily in the generations after establishment in the laboratory, showing convergence to the values of a long-established population serving as a control

(maintained in the lab for 24 generations before the foundation of the new one); the fecundity of the new population became similar to that of the long-established population after just 14 generations of adaptation to the laboratory. In this no man's land between the wild and the laboratory, the population evolved extremely rapidly. Instead of straining for dubious interpretations of the uncertain results afforded by studies of recently sampled populations, we might use the gap between the wild and the laboratory as an evolutionary tool—recognizing that, after all, the lab is just another environment to which populations adapt, albeit a very peculiar one.<sup>10</sup> To this extent, we can agree with Harshman and Hoffmann.

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## Reply from L. G. Harshman and A. A. Hoffmann

It has been argued that laboratory evolution experiments are superior to comparative studies<sup>1,2</sup> and phenotypic manipulations<sup>3</sup> for the study of evolution. It has also been argued that there are constraints on the design of most field evolution studies compared with laboratory evolution experiments,<sup>3</sup> and suggested that interpreting the results of field evolutionary studies is problematical relative to laboratory evolution experiments.<sup>3</sup> However, a crucial perspective on laboratory evolution studies calls these points of view into question. As we discussed in our recent *TREE* article,<sup>4</sup> there is a range of problems associated with laboratory selection experiments using *Drosophila* to study the evolution of life history and stress-related traits. In their letter, Matos et al.<sup>5</sup> did not significantly address any of the issues we raised.<sup>4</sup>

Their reply<sup>5</sup> is a bit puzzling because their argument is similar to the one we presented.<sup>4</sup> Like us, they describe the problem associated with conducting selection experiments using populations recently established in the laboratory. Specifically, we stated that “There is some evidence that *Drosophila* can adapt rapidly to laboratory culture,<sup>6</sup> reducing the concern about using populations maintained in the laboratory for only a short term. Nevertheless, it is unclear how many generations are required to dampen any spurious correlations potentially generated by domestication. To illuminate this issue, it is important to investigate the process of *Drosophila* domestication in terms of the time course of changes in life history and of stress-related traits, and to investigate the patterns of genetic correlations among traits.”<sup>7</sup> Once we have such information, it can be used as a basis to decide how long to maintain populations in the laboratory before initiating selection experiments; recommendations can be made about any likely confounding effects; and general guidelines could be established for comparing recently established and long-established populations. In this context and with a retrospective emphasis on “relatively,” we suggested that “Ideally, it might be desirable to conduct separate selection experiments on a long-standing equilibrium population and on a population derived relatively recently from the field.”

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