ECOLOGY

A Checkered History

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On the Wings of Checkerspots
A Model System for Population Biology
Paul R. Ehrlich and Ilkka Hanski, Eds.
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The spring day in 1960 when Paul Ehrlich caught his first bay checkerspot, *Euphydryas editha*, on Jasper Ridge in California was perhaps the butterfly ecology equivalent of Thomas Hunt Morgan bottling his first *Drosophila melanogaster*. Up until then, population ecology had tended to concentrate on very common species or those with boom and bust population cycles, and Ehrlich was looking for an unexceptional study organism with small, stable populations that would exemplify a "normal" species. He could hardly have envisaged that this butterfly would mark the beginning of over 30 years of intensive study of related species on both sides of the Atlantic. *On the Wings of Checkerspots* documents that research effort, which focused primarily on two species: *E. editha* in North America and the Glanville fritillary, *Melitaea cinxia*, in Europe. Sadly, the story also includes the eventual extinction, in the late 1990s, of the bay checkerspot populations at Jasper Ridge.

It is only by understanding the natural history of a species that general ecological theory can be tested in the wild. As an example that is discussed in the volume, there is a considerable theoretical literature on the impact of spatial habitat heterogeneity on population dynamics and persistence, but only scarce empirical evidence relates to this problem, much of it provided by checkerspots. On the Åland Islands in Finland, *Melitaea cinxia* has two major hosts, *Plantago lanceolata* and *Veronica spicata*. Local patches tend to be dominated by one or the other, leading to a heterogeneous patchwork of habitats. Many years of detailed annual censuses in this connected network of butterfly populations have led to the development of models that can be used to investigate the impact of this spatial heterogeneity on population extinction and colonization (*1*). It was found that an empty patch dominated by *Plantago* was more likely to be colonized by *M. cinxia* if the surrounding patches were also dominated by that host plant, and the equivalent pattern was found for *Veronica* patches. Experiments demonstrated that this differential success is due to local adaptation of butterflies in their host preferences (*2*). (In retrospect, it is perhaps unsurprising that if colonists are better adapted to the local conditions when they arrive at a patch, then they are more likely to establish a new population.)

This apparently simple result has far-reaching implications. Consider a network in which 80% of the checkerspot populations live in patches dominated by *Plantago* and 20% in *Veronica*-dominated sites. The *Veronica*-adapted genotypes can only persist if patches of their preferred habitat are sufficiently close to one another for frequent recolonization. If these patches are all isolated by surrounding *Plantago*, then the *Veronica*-adapted genotypes are likely to go extinct on a regional scale. The host-plant preferences also affect the survival probability of the whole system, because by making the *Veronica* habitat unavailable, the overall carrying capacity of the network is only 80% of what it could have been under a different spatial distribution of patches. Thus understanding the specific details of how *Melitaea cinxia* adapts to its hosts provides an elegant demonstration of how habitat heterogeneity impacts both the genetics of local adaptation and the probability of population survival.

Although the Jasper Ridge populations of *Euphydryas editha* came to a sorry end, it is to be hoped that their demise was not entirely in vain. There has been a strong emphasis on understanding population survival and extinction in checkerspot research that should be heeded by conservationists. For example, the repeated patterns of population extinction and colonization that have been so well documented in the Åland islands make it possible to separate the many factors that influence extinction risk. In particular, the relative influences of genetic and demographic factors on extinction are beginning to be understood in this system (*3*). This book should be required reading for all conservation biologists.

Furthermore, future butterfly ecologists will be inspired by the detailed observations of checkerspot natural history, which provide some of the most entertaining aspects of the volume. My favorite was Mike Singer's description of female *Euphydryas editha* dropping to the ground like stones and probing around hopelessly for nonexistent low-growing leaves on which to lay their eggs. This comic tragedy was the result of a recent host switch from the low-growing lousewort *Pedicularis semibarbata* to the erect annual *Collinsia torreyi*. Both species provided the chemical stimulus for oviposition behavior, but only the former has the low-growing leaves to which the butterflies are behaviorally adapted. The elegance of adaptation is easy to take for granted until things go wrong.

Threatened model metapopulation. The bay checkerspot (*Euphydryas editha bayensis*) inhabits sunny open grasslands in the San Francisco Bay area.

Studies of the checkerspot butterflies have provided major contributions to evolutionary and ecological theory over the last 30 years, notably in the fields of insect-plant coevolution and population dynamics. The editors and contributors have managed quite an achievement in bringing this work together with an overview of many aspects of checkerspot biology (including larval biology, reproductive dynamics, population genetics, phylogenetics, and comparative analysis). Furthermore, although the book is an edited volume with 15 contributors, it was obviously well planned and reads more like the work of a single author. Its structure could be a model for anyone wanting to write an overview of their particular research system. I strongly recommend *On the Wings of Checkerspots* to anyone interested in evolution, ecology, or entertaining and informative stories about butterflies.

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References
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