ECOLOGY AND EVOLUTION

Learning from Lepidoptera

Nina Wedell

What have overpopulation and butterfly research got in common? According to Paul Ehrlich's introductory chapter in *Butterflies: Ecology and Evolution Taking Flight*, butterfly researchers can help save the world from being overrun by mankind. Ehrlich (a cofounder of Zero Population Growth, now renamed Population Connection) believes lepidopterists have a responsibility to educate the public about human impacts because of the great appeal and popularity of butterflies. He has a point; butterflies capture the public imagination and are frequently used as metaphors to illustrate disparate phenomena: the butterfly effect in chaos theory, the Lorenz butterfly in nonlinear dynamics, and even "butterfly economics"—a new general social and economic theory.

Butterflies
Ecology and Evolution Taking Flight
by Carol L. Boggs, Ward B. Watt, and Paul R. Ehrlich, Eds.
University of Chicago Press, Chicago, 2003. 757 pp. $110, £77. ISBN 0-226-06317-8. Paper, $45, £31.50. ISBN 0-226-06318-6.

Butterflies, a multi-authored volume edited by Carol Boggs, Ward Watt, and Ehrlich (all biologists at Stanford University), illustrates the versatility of butterflies as model organisms. The 26 chapters are placed in five topical sections (each of which begins with a short overview): behavior, ecology, genetics and evolutionary dynamics, systematics and species diversification, and conservation and biodiversity. The volume, which grew out of the Third International Butterfly Ecology and Evolution Symposium (held at Mt. Crested Butte, Colorado, in 1998), combines newly reported research with reviews and syntheses, and the editors have taken great care to shape the collection into a coherent whole.

The high profile of butterflies among researchers is not a new phenomenon. Many famous lepidopterists have made substantial contributions to the study of evolution and ecology. Darwin himself used butterfly examples to illustrate the process of sexual selection (*1*). Commenting on the fighting of Emperor butterflies, he wrote "although butterflies are such weak and fragile creatures, they are pugnacious." He was also impressed by the brilliant colors of butterflies, which he believed were used by males to woo mates: "I am led to suppose that the females generally prefer, or are most excited by the more brilliant males." And he went on to suggest that butterflies have "sufficient mental capacity to admire bright colors." Christer Wiklund, Erika Deinert, and Hans Van Dyck develop the theme of sexual selection in their chapters.

Other heavyweight lepidopterists include J. B. S. Haldane, whose work in the field culminated in his eponymous rule (*2*), which predicts that in hybrid butterflies females (the heterogametic sex) should show greater inviability than males. In his chapter on molecular systematics, Felix Sperling notes that X-linked genes and mitochondrial DNA are particularly good markers of species boundaries, which makes butterflies ideal models for studies of speciation. Chapters by Richard Vane-Wright and by Dana Campbell and Naomi Pierce demonstrate the use of molecular genetics to unravel the relationships among butterfly groups.

An editor's choice. Boggs's chapter on the effects of variation in food resources draws on her studies of the Mormon fritillary, *Speyeria mormonia*. Human alterations of this North American butterfly's montane grassland habitat can have either negative or positive effects on food supplies. Grazing by cattle or sheep can remove favored hosts, whereas the introduction of exotics such as thistles can increase flower availability.

The father of ecological genetics, E. B. Ford, studied genetic polymorphisms (such as wing spot variation in *Maniola* satyrids) in the field (*3*). Watt's chapter on temperature adaptation demonstrates the tractability of butterflies as field models, and Paul Brakefield and Antónia Monteiro's work on butterfly eyespots continues the topic of wing patterns. R. A. Fisher and Ford published the original mark-release-recapture method using a moth (*4*); as Nusha Keyghobadi and co-workers demonstrate, the method retains a place alongside modern molecular techniques for estimating population size. Similarly, H. B. D. Kettlewell's classic study of evolution in action on melanism of the peppered moth and Darwin's pondering about mimicry are echoed in Richard ffrench-Constant and Bernhard Koch's studies on melanism in swallowtails.

Studies of butterflies as indicator species are increasingly playing a role in conservation efforts. Claire Kremen and her co-workers illustrate their importance in the design of Madagascar's Masola National Park; chapters by Camille Parmesan and by Jane Hill and co-workers show the value of butterflies in studies of climate change.

In their concluding overview, Watt and Boggs echo Ehrlich's theme of the pivotal role butterflies have in environmentalism. They also suggest research areas in which butterflies can become even more useful model organisms. For example, because butterflies are amenable to laboratory studies (with all the benefits this entails, particularly in regards to genetic dissection of traits), they offer an ideal system for examining interactions among genotype, phenotype, and environment. I also expect much progress from using butterflies in empirical tests of new theories. With their unusual sex-determination mechanism and the large fitness effects of their X-linked genes (*5*), butterflies offer an ideal system for examining recent hypotheses from sexual conflict theory that predict a role for the X chromosome as an attractor of sexually antagonistic alleles (*6*, *7*). Similarly, the suggestion that rare alleles for male traits and female preference are protected against random loss in male homogametic systems (*8*) is waiting to be tested.

Butterflies: Ecology and Evolution Taking Flight exemplifies the contribution lepidopterists have made to our understanding of the natural world. It is a testament to butterflies themselves that they can maintain such a carefree appearance whilst carrying so many of the secrets of the universe.

The reviewer is in the Ecology and Evolution Group, School of Biology, University of Leeds, Leeds LS2 9JT, UK. E-mail: n.wedell@leeds.ac.uk

References

1. C. Darwin, *The Descent of Man, and Selection in Relation to Sex* (John Murray, London, 1871).
2. J. B. S. Haldane, *J. Genet.* 12, 101 (1922).
3. E. B. Ford, *Ecological Genetics* (Methuen, London, 1964).
4. R. A. Fisher, E. B. Ford, *Heredity* 1, 143 (1947).
5. F. A. H. Sperling, *Can. Entomol.* **126**, 807 (1994).
6. W. R. Rice, *Evolution* **38**, 735 (1984).
7. J. R. Gibson, A. K. Chippindale, W. R. Rice, *Proc. R. Soc. Ser. B* **269**, 499 (2002).
8. H. K. Reeve, D. W. Pfenning, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 1089 (2003).