1 • Ecology of butterflies in Europe – where are we now and where to go?

ROGER L. H. DENNIS

To understand where we are now with butterfly research, and where to go next, we need first to clarify what we are 'about'. Inevitably opinions will be as varied as there are individual perspectives; we study butterflies for different reasons, but I doubt for one moment that any of us would belittle the contribution of those who study them simply for the joy of it – much of our knowledge base is founded entirely on enthusiasm for butterflies and our own research is fired by butterfly aesthetic beauty. A little more grist to the mill can be applied by trying to qualify objectives with purpose; butterfly research these days can no more escape an economist's cost–benefit analysis than anything else that is funded. Even so, it brings focus to what we do, to consider human benefits other than our own, and some like me would argue that we have an obligation, a duty, to future generations to do so. So, what should we be 'about'? Butterfly research has already provided the answer. Exponential human population growth conjures up visions of massive planetary changes, among them biome losses, ecosystem failures and climatic shifts, all with serious consequences for humanity itself: starvation, disease, disaster and warfare press home that despite technological advances, globally things are going seriously amiss. Butterflies, along with other biota, provide sufficiently sensitive barometers for monitoring the changes and predicting such outcomes in their initial stages (Thomas 2005); they are signposts to human well-being, indicators of environmental changes and ultimately with losses in other organisms herald a pending global extinction crisis of geological proportions and failure in sustainability. Aside from this vital role, butterflies are model organisms for numerous research areas in biology (Ehrlich & Hanski 2004), extending from physiology and development, gene–environment interactions, population and spatial dynamism, ecological order, community organisation to key themes in evolution, particularly speciation. They do so owing to their unique combination of attributes: their widespread occurrence throughout biomes, variation in abundances and range sizes, their short, discrete generations but variety of life histories, their array of patterns, diversity of taxa, multiplicity of species, their rapid response to conditions and assortment of adaptive modes for different aspects of phenotypes, variation in mobility, variety of habitat scaling and sheer aesthetic beauty. As such, not only do they present a variety of sensitive markers for environmental change at different scales and for different purposes, but are easily recognisable, attract attention, have wide popular appeal, are sufficiently numerous to be easily monitored using simple methods and can therefore be recorded at low cost.

It is hardly surprising then that the scientific literature on butterflies dating back to the nineteenth century is extensive and growing rapidly. The present book (EBIE) is another, important milestone along the path to understanding them. It runs in the vein of thematic texts dealing with topics and issues in butterfly biology and has direct predecessors in *The Ecology of Butterflies in Britain* (EBIB: Dennis 1992a) and *The Biology of Butterflies* (Vane-Wright & Ackery 1984), both founded on E. B. Ford's *Butterflies*. More recent specialist texts are *Butterflies: Ecology and Evolution Taking Flight* (Boggs *et al.* 2003) and *On the Wings of Checkerspots* (Ehrlich & Hanski 2004). These thematic books have counterparts in systematic texts which provide detailed accounts species by species. Thus, EBIB was married to *The Butterflies of Great Britain and Ireland* (Emmet & Heath 1990), *The Millennium Atlas of Butterflies in Britain and Ireland* (Asher *et al.* 2001) and *The State of Butterflies in Britain and Ireland* (Fox *et al.* 2006). For EBIE, there is as yet no direct partner covering the continent's butterfly fauna, but a most exacting model is Frits Bink's (1992) *Ecologische Atlas van de Dagvlinders van Noordwest-Europa* a painstaking audit of attributes of north-western European species. Nevertheless, continent-wide texts are growing in number and the details they convey (Tolman & Lewington 1997, Lafranchis 2004). In the UK, species' distributions are effectively illustrated in the systematic texts; in Europe, this is a singular, independent entity, *The Distribution Atlas of European Butterflies* (MEB: Kudrna 2002) with a second edition soon to be forthcoming. Both EBIB and EBIE are underpinned by numerous regional texts and atlases. In the UK, these take the form of county or multiple county

Ecology of Butterflies in Europe, eds. J. Settele, T. Shreeve, M. Konvička and H. Van Dyck. Published by Cambridge University Press. © Cambridge University Press 2009, pp. 1-5.

treatments and a single national text for Scotland (Thomson 1980). On mainland Europe an increasing number of books for individual countries is emerging, splendid in production, revealing in details, invaluable for data, many with thematic cores, engaging contexts and condition of the fauna (e.g. Henriksen & Kreutzer 1982, Geiger 1987, Stoltze 1996, Maes & Van Dyck 1999, Lafranchis 2000, Settele *et al.* 2000). Many texts are appearing for the countries once making up the Soviet Union, including Russia itself (e.g. Tuzov *et al.* 1997, 2000), and a growing number of colourful texts covering smaller regions and islands are appearing (e.g. Lake Garda region: Sala 1996; Schleswig-Holstein: Kolligs 2003; Cyprus: Makris 2003). On other continents, there are parallel, if less advanced, developments (USA: Scott, 1986; Australia: Braby 2001).

EBIE is built on the same pattern as EBIB. Throughout the text there is a shift from individual behaviour through populations to species and communities, and from ecological-scale issues to evolutionary-scale outcomes. The book too has as its crux, conservation. Indicators butterflies most certainly are, but such urgency as exists to conserve the indicators themselves impresses on us all that the trends are not being taken seriously enough or being adequately reversed by politicians and policy makers. Nevertheless, the differences that are evident between the two books are a measure of what has been achieved over the past one and a half decades. In several respects EBIE moves towards an order of magnitude larger than EBIB – in words, concepts, authors, references, ecological intimacy, model intricacy and evolutionary reach; all this reflects on the shift in focus from island to continent – in spatial scale, altitudinal range, biomes and in climate. There is also the expanding perspectives of researchers from different countries, cultures, contexts, facing different crises, each bringing their variety of talents and reminding us of work done by our predecessors closed off to us in the past by barriers of language and limits to intellectual exchange – the impressive work of Petersen (1947) on morphology gradients, Kostrowicki (1969) on faunistic patterns, Warren's (1926, 1936) monographs on the Hesperiidi and *Erebia*, and Lorkovic's extensive practical work on speciation, just four examples among many. In detail, a glance through the contents reflects three basic changes, advances in EBIE: many topics in EBIB now have their own chapters in EBIE (i.e. adult feeding, mate location behaviour, oviposition, thermoregulation, spatial gradients in attributes and species richness); others have been substantially updated with new models, findings and viewpoints (i.e. population structure and dynamics, dispersal, population genetics, functional significance of wing morphology, conservation status). In EBIE, readers will find defence of and merit argued for some older concepts (e.g. subspecies in Chapter 16; faunal elements in Chapter 17), but a key feature is the advent of new research areas; such are predictive species modelling, population spatial structure and dynamics, parasitoids, the evolutionary ecology of fecundity, speciation, and responses to climatic warming. The findings on wing morphology–behaviour–substrate relationships promise an exciting future for research, the result of many years of data collection by Tim Shreeve and his team (Chapter 13). In EBIB we looked back to the Pleistocene glaciations to account for evolutionary adaptations and gross distributional patterns. Following the projections of climatic change on butterfly populations (Dennis 1993), in EBIE, the vantage is forwards to predict the outcome. Retrodictions, though fascinating in providing evolutionary perspective (Dennis 1977, 1993), are hamstrung by the ultimate lack of fossil proof; in direct contrast, predictions are directly testable and germane to the current biodiversity crisis (see Chapter 20). There is also a greater readiness in this new text to explain techniques and give direction (e.g. Chapter 7: Predictive species modelling; Chapter 19: Hybrid zone analysis; Chapter 22: Population viability analysis). With the increased sophistication in methods, this is essential. In each chapter the reader will find guidance to potential research areas: no Ph.D. student in butterfly biology can declare he/she lacks problems to solve; the contrary perhaps, they may well be overwhelmed with several lifetimes of work to be done.

Advances in EBIE and future direction can perhaps be best sought through consideration of three ploys: expansion of data and knowledge, development of models and experiment, and construction of explanatory systems. The reality of models and the completeness of systems depend on the quality of data on butterfly biology.

At its simplest 'data' is another word for the knowledge or information we can acquire on an object of interest. It is the data that have accumulated on butterflies that make them such valuable indicators of change and model organisms for evolutionary studies. Data for diverse taxa have spawned groups, distinct in life history, that act as markers for discrete processes (e.g. migrants that flag up an increase in aliens and climatic changes, specialists that warn of landscape fragmentation, generalists that monitor landscape toxicity). A prominent feature of EBIE is the signalling of an exponential increase in knowledge in butterfly biology; inevitably, therefore, some tasks highlighted in EBIE are already in progress (e.g. species diversity on European islands: Dennis *et al.* 2008a, Dapporto & Dennis 2008a, b) and making a difference for conservation – as a result of Leonardo Dapporto's biogeography work, butterflies have been given priority within the vicinity of Monte Capanne on Elba within the Legambiente, and the National Park of the Tuscan Archipelago and the Italian energy agency (ENEL) have funded the project. Much of the development in butterfly biology is in the demonstration of links and associations among traits or between traits and environmental agents (e.g. Chapter 2: nectar use; Chapter 6: modes of thermoregulation; Chapter 10: genetics; Chapter 12 and 13: morphology and environment; Chapter 14: fecundity; Chapter 15: gradients). A growing trend is the development of species databases (Chapter 5: larval host plants; Chapter 11: parasitoids). It cannot be emphasised enough how important database development is on butterflies, as for other organisms: their co-ordination, centralisation, documentation and universal access (Dennis *et al.* 2008b). Currently, the accumulation of data is uneven and some aspects of butterfly biology are poorly known (e.g. butterfly roosts, hibernation sites, flight threshold temperatures, use of scent and sight for interactions and resource use, wing patterning, impact of pathogens). Database development is also being unnecessarily duplicated by different research groups (host plants, nectar sources, phylogenies) and there is both lack of direction and universal access, especially to atlas databases, despite the fact that these data have been supplied by the goodwill of myriads of recorders. The most crucial aspect of databases for future progress is the quality of documentation. Although the key feature of butterflies is their space-time variability, most data on traits in butterfly biology lack explicit space-time co-ordinates. Much as it is unthinkable that museum specimens, atlas and monitoring scheme records exist without data for location and time, so too should it be equally inconceivable for data on resource use, behaviour, life history, phenotypic differences and all else to be bereft of such basic recording fields. Spatial and temporal variability are key aspects of butterfly biology; without a space-time context for observations (e.g. for nectar feeding, host use) comparative studies lack the most vital components of that variability that makes them effective indicators and model organisms. Turning this around, behaviour and substrate use of observed butterflies firms up the status of atlas and monitoring scheme records (Dennis 2004, Dennis *et al.* 2008b).

A crucial part of developing future databases is adequate sampling strategies, as urged by Mark Shaw and his colleagues for parasitoid records. Despite the failure of atlases to achieve universal cover even over relatively small regions such as the UK, there is still a reluctance to be weaned off the aspiration of continuous recording cover. Faced with the vast territory of Europe, the expanding conservation activity in its component states and the need for continually updating spatial records of species at finer scales, this is an issue that national conservation organisations and co-ordinators of atlases will inevitably have to confront, particularly if we move to establishing better the status of the records we are making (Dennis *et al.* 2008b). A key to developments is the adoption of stratified, fixed sampling designs and nested studies. Another part of this process of data acquisition is adequately defining terms. Some concepts are elusive and readers should give close attention to the call for pragmatic solutions as Descimon and Mallet (Chapter 16) have done for designation of species; as discussed below this is highly relevant to conservation which ultimately depends on identifying an appropriate unit, the habitat.

An essential part of the sampling strategy for data is regional development, that is, development of butterfly biology throughout more European states – a primary aim being that more regional work generates more data on spatial variation in species traits. EBIE demonstrates well that this is fast happening with many new centres for research. In 1972 when I was hoping to convert undergraduate observations on the Creuddyn Peninsula in North Wales to a Ph.D. studentship, I was informed that there was not a single institute in the UK that could provide 'adequate supervision'! Now, young researchers can look to Sweden, Norway, Britain, Holland, Belgium, France, Germany, Spain, the Czech Republic and many other countries, for centres, multiple ones in some states, to engage in butterfly research. A key to regional development, however, goes beyond research centres or organisations, to enthusing popular interest. This has formed the foundation of success for Butterfly Conservation UK and there is no reason why it should not spread to other parts of Europe. Many more students are now emerging from new universities, trained in the biological sciences with a deep interest in nature. They may not have careers in butterfly biology, and have busy lives in their own professions, but their training, coupled with their interest, especially when they are released at retirement, is an energy and knowledge we would do well to harness. Many others have no training in biology at all, but they bring a variety of other skills and their capacity for advancing butterfly conservation and biology should not be underestimated or overlooked. If we want to build up databases of butterfly sites, resources, behaviour, life history elements over the length and breadth of a continent, and firm up the platform for butterfly conservation, the starting point is to encourage the current and future generations to take part in the quest; the list of acknowledgements at the end of the parasitoid chapter is an indication of what can be achieved.

A significant advance for butterfly biology evident in EBIE is the development of models (aids for thinking and analysis): statistical, explanatory, experimental and predictive, many simulated in computer-driven algorithms. In the last two decades predictive modelling has become most prominent in spatial population dynamics owing to the superlative research by Ilkka Hanski and colleagues on Åland island butterflies such as *Melitaea cinxia*. These models have formed the basis for modern thinking in conservation, a move from single to multiple population units. In EBIE, we see the beginnings of the dialogue generating hybridisation between metapopulation models and landscape models; chapters on 'Predictive species modelling in butterflies' by Boris Schröder and colleagues (Chapter 7), metapopulation dynamics by Robert Wilson and David Roy (Chapter 8), and population viability analysis (PVA) by Nicolas Schtickzelle and Michel Baguette (Chapter 22) are particularly important. Link these up with landform influences on butterfly geography and conservation (Dover & Settele 2008). Another important area for modelling is projection of the impact of climate change and biotope fragmentation on species dynamics (persistence, range expansion, extinction). The historical branch of this does not escape scrutiny; retrodiction for evolutionary history cannot rely entirely on a molecular clock for determining vicariance, origins and dispersal pathways; to do so would be to fall into the same trap disparaged by this author in early attempts to determine origins of butterflies into Britain based on species' ('racial') physical distinctions (Dennis 1977). All these new approaches, sets of models, require a new interpretation of habitats involving a shift from simple notions of habitat equating with vegetation units to species resources (complementary resource use). Engaging finer resource units is the real ecological equivalent – not niche which lacks spatial co-ordinates – of subatomic particles to the atom in physics; much as physicists wouldn't think now of truncating their lower limit of attention to an atom, no longer can ecologists restrict their thinking to a vegetation unit as habitat. Referring to a biotope as a species' habitat is as bad as referring to that species by its higher taxon, or worse still, naming it as a mix of two or more higher taxa. Fractionation to finer units will become a feature of butterfly biology; it is an inevitable part of moving issues to finer resolutions, of attaining greater accuracy and precision and of making better predictions. Such models are expected to become space-time explicit and depend on parameters generated from acquisition of space-time explicit data.

A parallel trend is that statistical modelling is becoming a great deal more sophisticated. The distinction between appropriate and inappropriate designs is becoming blurred by multiplicity in approaches and alternative methods. Adjustments for bias are now commonplace, dealing with problems of spatial autocorrelation, apparency, phylogeny and recording effort. We have reached a stage where we are forced to inquire whether the data we are collecting are apt and match the models for sophistication. Despite all this complexity, EBIE authors have provided a pain-free introduction to developments in thinking aids that will continue to grow; in this respect Chapter 7 on species predictive modelling is a splendid example.

The authors also disclose an increased preparedness to experiment and urge more to be done; for example, there is nothing in European butterflies to match the lifetime work on *Zygaena* genetics by Gerry Tremewan (2007) or on *Heliconius*. Experiment has long been integral to laboratory work (e.g. host choice in oviposition and herbivory; pheromone studies) and fieldwork (e.g. mark–release–recapture in population dynamics and dispersal); tests are essential to erase speculation. But, much as solutions cannot all be acquired through direct observation of nature, nor can they be achieved entirely through experiment – in several chapters it is revealed how experimental results are frustrated by interactions in real landscapes where real things happen. This should not deter experiments, just ensure that findings are transferred to real-world situations. In EBIE are accounts of simple but highly effective experiments to solve problems. Per-Olof Wickman describes the neat, ground-breaking example in the release of unmated females to determine mating cues (Chapter 3); as he demonstrates, direct observation cannot distinguish mated from unmated females which behave very differently. Another is the manipulation of wing morphology to test aspects of sexual and natural selection, a field greatly advanced by Paul Brakefield and his research team. John Dover and Garry Fry's (2001) use of artificial sightlines and obstacles to study corridors and barriers is delightfully inventive. EBIE introduces burgeoning ingenuity in large-scale experiments – the use of outdoor (semi-natural) cages has been highly productive, already the generator of important papers (see

Cambridge University Press
978-0-521-76697-5 — Ecology of Butterflies in Europe
Edited by Josef Settele , Tim Shreeve , Martin Konvička , Hans Van Dyck
Excerpt
More Information

Chapter 12 and 14); I look forward to the next stage, the manipulation of whole landscapes to better understand the impact of landscape and habitat components on population persistence and integration.

We come now to a most important question; how are we going to make the best use of all this new knowledge? Sören Nylin (Chapter 15) makes the essential point: 'We are still far from a situation where we really understand how the environment shapes the features of butterflies and other organisms.' In my view this stems from a preoccupation with single functions, paired associations and simplistic notions of cause and effect. Hitherto, this has been necessary and invaluable; understanding starts from isolating key variables, establishing links, distinguishing proximal from distal agents and determining levels – bottom–up versus top–down. However, full understanding has to be more than this. Butterflies and their components are part of natural systems. In EBIB, I tried to draw attention to this issue by producing a number of simple process–response models and warned against 'tunnel' reasoning. The time has come for butterfly biologists to become systems biologists. This requires a dedicated, co-operative effort to hardwire the components influencing key issues in butterfly biology, to locate feedbacks, key switches, trade-offs, rheostats, synergisms and equifinal routes within systems; from this should emerge new principles. Only with this approach will it become evident why conundrums, the many unexpected results reported in the following chapters, happen and keep happening (e.g. sawtooth clines in size; inverse egg size – host quality relationships). Of course, this is not easy; butterfly biologists are faced with bundles of reaction norms (e.g. plastic responses), genuinely complex patterns and processes, and even the arsenal of supposedly heuristic multivariate techniques are no panacea or substitute for originality and insight. Butterfly biologists, then, have to be prepared for a future where at one end variables are being fractionated, finer definitions are being made, and at the other, links are coming together into structured webs. The idea is that running the systems in a computer will inform us how butterflies will 'behave' in different circumstances; we then build landscape experiments to check them out. In this process, it cannot be overemphasised how important it is to get the basic units right; if we do not select real units we will generate unrealistic expectations. That is why habitat as a vegetation unit has outlived its usefulness.

The primary objective in all this research is difficult for readers to miss; it is compounded in the four chapters of the last part on 'Global change and conservation'. There is a simple way of appreciating the crisis: we have long had water-deficient red deserts and energy-deficient white deserts; now we have species-deficient green ones – marinated in herbicide and fertiliser. Green deserts pave the way to ultimate sterility as red deserts. The notion is foreign to much of the public and many politicians who pay lip service to biodiversity. The European landscape is indeed productive, but in diversity of plants and animals quite moribund. It is inevitable that if butterfly biologists are to make a difference for future generations, then they will have to become political animals; they will be taken seriously only if the science is watertight, predictions are accurate and actions responsible ones. Faced with human demands and continual changes to land and climate, we need to find solutions where the natural world can be subtly dovetailed into an economic structure that works for long-term sustainability. In this process tests are everything and evidence-based procedures the Holy Grail (Pullin & Knight 2001). There are powerful arguments for maintaining diversity and heterogeneity; loss and blandness equates to erosion of genes and gene complexes, of naturally occurring chemicals and structures, of ecosystem stability, planetary resources and ultimately economic well-being and the human spirit. The threats are well known and addressed in the final chapters. To combat Europe-wide problems, a Europe-wide organisation becomes the lynchpin: to map, monitor populations, co-ordinate regional studies, to encourage co-operation among researchers and make best use of available talent, to accumulate sufficient resources, to tackle nested research programmes, and to press for apt legislation. Butterfly Conservation Europe aims to conserve butterflies and their habitats across Europe – from the above account, the reader will gather that this author feels that a first step is to be absolutely clear about what we mean by habitat. It is the context for populations, for evolutionary changes, between which individuals transfer, and the base for management. Unless we isolate the elements in habitat – resources and conditions – and understand how they impact on individuals, and amalgamate to integrate populations, our grasp of butterfly biology will remain deficient, artificial, in which case the identification of prime sites (Chapter 21), reconstitution of traditional techniques (Chapter 23) or adoption of political solutions (Chapter 23) will fail to have the desired effect.

ACKNOWLEDGEMENTS

Many thanks to Peter Hardy, Tim Shreeve and Tim New for their helpful suggestions.

Cambridge University Press
978-0-521-76697-5 — Ecology of Butterflies in Europe
Edited by Josef Settele , Tim Shreeve , Martin Konvička , Hans Van Dyck
Excerpt
More Information

Part I
Habitat use: resources and constraints

CAMBRIDGE
Cambridge University Press
978-0-521-76697-5 — Ecology of Butterflies in Europe
Edited by Josef Settele , Tim Shreeve , Martin Konvička , Hans Van Dyck
Excerpt
More Information

2 • Adult food resources in butterflies

ANDREAS ERHARDT AND JOVANNE MEVI-SCHÜTZ

SUMMARY

Adult butterflies can substantially increase their longevity, and in most cases fecundity, by engaging in feeding. For some species adult feeding supplements the resources gained during the larval stage, but for others it is critical for egg-production and ensuring mating success, being the most important for long-lived species and for females that emerge as adults with few or no developed eggs. Butterflies feed from a variety of resources, and, within species, males and females may differ in their feeding patterns and substrates exploited, as they have different energy and nutrient requirements. The most commonly used substrate is floral nectar, which varies in composition and quantity between and within species, according to location, flower age, time of day, weather and number of pollinator visits. However, besides nectar sugars, nectar amino acids seem to play a more important role for butterfly fecundity than so far acknowledged. Butterflies primarily find nectar resources using vision, and secondarily using olfaction. Species may vary in their colour preferences, but there is ample evidence that foraging involves learning, and the range of plants exploited by individuals may be limited by memory constraints, with individuals displaying constancy for particular flower types. Visited flowers tend to be upright, with long tubes, or spurs, and are most frequently radially symmetrical. Adult butterflies may be efficient plant pollinators and their selectivity may play a role in the persistence of particular plant species and influence the evolution of flower morphology. When adult flight periods coincide with the flowering time of their larval host plants there are strong advantages for adults to exploit the nectar of their host plants. The spatial coincidence of larval and adult resources leads to the simplification of search images for adult food resources and egg-laying locations and the possibility that adult feeding ensures the reproduction of the larval host plants. Adult food resource distribution plays a key role in determining habitat quality and the suitability of landscapes for butterfly persistence; food resource quality and distribution play important roles in the dynamics of butterfly populations.

FOOD USE OF BUTTERFLIES AND CONSTITUENTS OF THESE FOOD SOURCES

Adult butterflies spend a great proportion of their lives foraging for and feeding on a broad variety of resources. The utilization of various nutrient sources by butterflies depends on the availability of resources at any given time or site (Brakefield 1982, Dennis 2004, Tudor *et al.* 2004). Weather, anthropogenic habitat alteration and competition for nutrients can result in variation of food quantity and quality. Basically, butterflies require water, carbohydrates, proteins, the essential amino acids (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine), sterols, vitamins and minerals such as sodium, magnesium, calcium and phosphorus. Some of these requirements may be met, or partly met, in the larval stages, but adult feeding is known to contribute to adult energy requirements, longevity and reproductive success. Adult requirements may differ between species and also between sexes, but for the majority of species adult feeding is essential for success.

Floral nectar is by far the most common and widespread butterfly food source (Norris 1936, Gilbert & Singer 1975, Boggs 1987). The chemical composition of floral nectar is highly variable, with different plant species producing different quantities and various constituents (Baker & Baker 1983). These differences include the concentration and composition of sugars, amino acids, lipids, vitamins, alkaloids, phenolics and glycosides (Baker & Baker 1975, Baker & Baker 1977, Baker & Baker 1983, Rusterholz 1998).

Butterflies are able to utilize several components of nectar. Water is the primary constituent of nectar, with sugar concentrations ranging between 15% and 53% (Baker & Baker 1983, May 1985, Rusterholz 1998). Sucrose, fructose and glucose are the three main sugars in nectar and butterfly-pollinated flowers are characterized by high proportions of sucrose compared to fructose and glucose (Baker & Baker 1983). Amino acids, the building blocks of proteins, are found in higher concentrations in butterfly-visited

Ecology of Butterflies in Europe, eds. J. Settele, T. Shreeve, M. Konvička and H. Van Dyck. Published by Cambridge University Press. © Cambridge University Press 2009, pp. 9-16.

flowers compared to bee-visited flowers (Baker & Baker 1975). In addition, nectar amino acid composition shows a high degree of constancy within plant species, perhaps giving the nectar a distinct taste, thus making it recognizable for specific butterflies (Baker & Baker 1977, Gardener & Gillman 2001). All ten essential amino acids are found in the nectar of one plant species or another, as well as several quasi- and non-essential amino acids. The amino acids alanine, arginine and hydroxy-proline are present in almost all nectars, and asparagine, proline, serine, threonine and glycine are also common (Baker & Baker 1975, Gottsberger *et al.* 1989, Lanza *et al.* 1995, Rusterholz 1998).

The quality of nectar can change depending on flower age, time of day, weather and activities of previous nectar feeders (Corbet 1978, Gottsberger *et al.* 1990). Adult nectar stress within butterflies may be quite common due to plants' responses to weather conditions; high temperatures and low humidity can cause evaporation of water thus making the nectar too viscous to extract, whilst rain can dilute nectar (Boggs 2003). Furthermore, the expected rise in atmospheric CO_2 concentration has been shown to reduce the amount of nectar and alter the amino acid composition of some plants (Rusterholz & Erhardt 1998; but see Lake & Hughes 1999 and Erhardt *et al.* 2005). Pollen contamination of nectar caused by pollen being knocked into the nectar by floral visitors has profound effects on nectar. The resultant increase in amino acid concentration provides an even greater reward for butterflies (Erhardt & Baker 1990, Gottsberger *et al.* 1990).

Pollen provides certain species in the Neo-tropical *Heliconius* genus with amino acids and proteins (Gilbert 1972, Dunlap-Pianka *et al.* 1977, Boggs 1981a). Deliberate pollen feeding was also suggested for Neo-tropical *Parides* and *Battus* butterflies (DeVries 1979), but is not known to occur in other butterfly genera.

Adult butterflies are known to use a wide variety of food sources aside from nectar and pollen. Puddling is a common activity where primarily male butterflies frequent mud puddles, edges of ponds, damp sand, carrion and animal dung (Adler & Pearson 1982, Pivnick & McNeil 1987, Sculley & Boggs 1996, Beck *et al.* 1999, Hall & Willmont 2000). Males acquire nutrients such as sodium, potassium, trace elements and possibly also organic and inorganic nitrogenous compounds (Arms *et al.* 1974, Gilbert & Singer 1975, Boggs & Dau 2004). Rotten fruit, though more common in tropical climates, also attracts certain butterflies. Fermenting fruit offers a variety of nutrients including sugars, proteins and in some cases ethanol (Norris 1936, Brakefield 1994, Braby & Jones 1995, Miller 1997). Honeydew, the sweet secretion from aphids, is an alternative source of nourishment for both male and female butterflies and particularly among woodland butterflies (Norris 1936, Porter 1992). However, the ingestion of honeydew from polluted leaves may adversely affect butterfly populations (Corke 1999). Butterflies occasionally alight on perspiration and saliva in search of water and salts, and in at least one case appear to prefer saliva over a sugar solution (Tumler 1885, Norris 1936, Arms *et al.* 1974). Additional, less commonly used resources include tree sap, wood ash, litter, dry earth, rotten plants, stones, ant-bird droppings, fungal exudations on grass flowers and in one documented case the blood of a wounded horse (Seitz 1894, Norris 1936, Ray & Andrews 1980, Brown 1984b, Shreeve 1992b). These resources provide the butterflies with various proteins, minerals and in some cases secondary metabolites used for defence against predators.

Furthermore, water, in the form of water droplets on plants, as well as being acquired through puddling, nectar intake and a variety of food sources, is essential for butterflies (Norris 1936, Watanabe 1992, Braby & Jones 1995, Miller 1997).

EFFECTS OF FOOD ON SURVIVAL AND REPRODUCTION

Life history strategies, including the number of generations per year, duration and timing of each developmental stage, number and size of offspring and longevity, are affected by both larval and adult feeding (Boggs 1987). Some butterflies emerge with all eggs yolked, whereas other species have only a few or no eggs ready upon emergence. Adult feeding becomes increasingly important for egg production in those long-lived species which emerge with few or no eggs (Leather 1995). Furthermore, there is a clear link between butterfly biological traits, resource use and host plant strategies (Dennis *et al.* 2004, Stefanescu *et al.* 2005b). Nutritional resources allocated for longevity and fecundity by butterflies are obtained in three ways: (1) larval uptake and storage in fat bodies, (2) adult feeding, and/or (3) nuptial gifts (male nutrient investments passed to females with sperm via the spermatophore at mating) (Boggs 1981a, Boggs 1990).

Nutrients acquired during larval development were believed to be the primary determinant of longevity and fecundity in butterflies, especially in those which do not feed as adults (Labine 1968, Dunlap-Pianka *et al.* 1977, Boggs 1987, Svärd & Wiklund 1988a, Baylis & Pierce 1991, Karlsson 1998, García-Barros 2000c, Hughes *et al.* 2000).

However, the role of adult nutrition in many butterfly species, in the form of direct uptake or as nuptial gifts, may be of substantial importance in determining longevity and fecundity in butterflies. Norris (1935), a pioneer in this field, showed that longevity and fecundity in *Pieris rapae* was greatly increased by adding sugar to water. The addition of sugars to adult food has been shown to increase longevity and fecundity in a number of other species (Stern & Smith 1960, David & Gardiner 1962, Murphy *et al.* 1983, Leather 1984, Moore & Singer 1987, Hill 1989, Hill & Pierce 1989). There is a significant increase in the number of mature eggs produced by *Papilio xuthus* L. when the females were fed sugar solutions (Watanabe 1992) and adult feeding in *Thymelicus lineola* can increase egg production by 27 times (Pivnik & McNeil 1985b). Rotting fruit and honeydew uptake have been shown to prolong female lifespan and oviposition rates (Miller 1989, Braby & Jones 1995). Adult fruit feeding is essential for the onset of oviposition in the tropical frugivorous butterfly *Bicyclus anynana* (Fischer *et al.* 2004b). Further studies have shown that adult derived sugars are incorporated into eggs and that in some cases may make up for 50–60% of egg carbon (Boggs 1997a, O'Brien *et al.* 2000).

The uptake and utilization of amino acids from pollen greatly increases the number of eggs and duration of egg laying in tropical pollen-gathering *Heliconius* species (Gilbert 1972, Dunlap-Pianka *et al.* 1977). Rotten fruit appears to supply females with an adequate supply of proteins to maintain constant egg production in *Mycalesis terminus* (Braby & Jones 1995) and radiotracer studies on *Speyeria mormonia* have clearly demonstrated that amino acids obtained in the adult stage are incorporated into eggs (Boggs 1997a). Honeydew, another nitrogen source, has also been shown to prolong female lifespan and enhance reproduction (Miller 1989). Despite this evidence, the role of nectar amino acids as a beneficial source of nitrogen for adult butterflies remains controversial. Although some butterfly species show a distinct preference for nectar containing amino acids, suggesting some form of dependency and utilization of this nectar constituent (Alm *et al.* 1990, Erhardt & Rusterholz 1998, Ruehle 1999, Rusterholz & Erhardt 2000, Mevi-Schütz & Erhardt 2003a, Mevi-Schütz & Erhardt 2004), the actual benefits of nectar amino acid have been difficult to demonstrate. Murphy *et al.* (1983) have shown that *Euphydryas editha* receiving amino acids lay larger eggs in later masses. These results were refuted by Moore & Singer (1987) who found no amino acid effect on the maintenance of egg weight over time for the same species. The presence of amino acids in food stimulated the butterfly *Jalmenus evagoras* to feed, but did not lead to an increase in longevity and fecundity, and amino acids in the adult food actually reduced fecundity in *Euploea core corinna* (Hill 1989, Hill & Pierce 1989). Amino acids in a *Lantana camara* nectar mimic fed to *Lasiommata megera* butterflies raised under benign greenhouse conditions had no effect on any of the measured fecundity parameters. Egg number and egg weight decreased at the same rate regardless of diet treatment (Mevi-Schütz & Erhardt 2003b). However, more recent work has shown that *Araschnia levana* raised under natural larval food conditions laid more eggs when they were fed nectar containing amino acids, whereas nectar amino acids had no effect on the number of eggs laid by butterflies raised on larval food rich in nitrogen (Mevi-Schütz & Erhardt 2005a). Therefore, nectar amino acids should be recognized as essential resources affecting butterfly fecundity and butterfly populations under natural conditions.

Puddling and the uptake of various nutrients, especially sodium, increase the number of matings of male butterflies (Pivnick & McNeil 1987). Males contribute indirectly to egg production by passing essential sodium and potassium to females at mating (Shreeve 1992b). Amino acids acquired during puddling were incorporated into somatic tissue of *Papilio glaucus* L. (Arms *et al.* 1974) and males receiving electrolytes plus amino acids fathered seven times more offspring than those that did not (Lederhouse *et al.* 1990). The attraction of male butterflies to nitrogen-rich resources such as rotting carrion and albumin baits suggests that these nutrients may increase reproductive success (Beck *et al.* 1999, Hall & Willmont 2000). Males pass a substantial amount of nutrients in the spermatophore to the female during mating (Rutowski *et al.* 1983) and these nuptial gifts are known to increase female longevity and fecundity (Kaitala & Wiklund 1994, Boggs 1995). Although larval reserves predominate in the first spermatophore, male butterflies utilize adult resources for multiple matings and reproductive potential is severely limited if adult feeding is restricted (Lederhouse *et al.* 1990). Female butterflies receiving a large first spermatophore have a higher lifetime fecundity and multiply mated females live longer, thereby utilizing a larger part of their reserves for egg production (Ward & Landolt 1995, Oberhauser 1997, Karlsson 1998, Hughes *et al.* 2000). Males and females may use different food sources depending on the demands of egg and sperm production. Trade-offs in either sex between adult feeding habits and the effects of large or multiple spermatophores on adult food preference have yet to be examined.

BUTTERFLIES AS POLLINATORS

Flowers from the viewpoint of butterflies

The perceptual mechanisms of butterflies to locate flowers include vision in the first place and to a lesser degree, olfaction (Boggs 1987, Omura *et al.* 1999, Andersson 2003, Andersson & Dobson 2003, Omura & Honda 2005). The visual spectral sensitivity of butterflies varies across taxa, but extends from ultraviolet to red in some species, the widest known among animals, including humans (Silberglied 1984, Weiss 2001). Butterflies have different innate colour preferences, which can vary between genera within a family, between species in a genus, and even between the sexes in a species (Weiss 2001 and references therein). For instance, the European swallowtail *Papilio machaon* has a clear preference for purple (Ilse 1928), whereas the New World papilionid *Battus philenor* strongly prefers yellow, with a minor preference for blue/purple (Weiss 1997). These different colour preferences may be related to sexual behaviour, although evidence for this is not unambiguous (Silberglied 1984). Possible evolutionary explanations could also include niche differentiation of different butterfly species for different flower types and/or evolved colour preferences for the main nectar plants in the primordial biotopes of the different species. Different floral colours could also be correlated with different types of nectar, which in turn could have led to the evolution of the observed colour preferences of butterflies.

Butterflies are often considered to be opportunistic foragers which visit a variety of available flowers (e.g. Sharp *et al.* 1974, Courtney 1986, Grundel *et al.* 2000). If a species produces more than one generation per season, different generations are likely to encounter different available nectar plants and have therefore to be opportunistic. However, butterflies do not visit flowers randomly, but often show distinct flower preferences which can differ between species and even between conspecific males and females, according to their different energy needs and reproductive requirements (Watt *et al.* 1974, Wiklund & Ahrberg 1978, Pivnic & McNeil 1987a, Erhardt 1991, Erhardt & Thomas 1991, Porter *et al.* 1992, Rusterholz & Erhardt 2000). Research in subalpine meadows in the Swiss Central Alps (Erhardt 1995 and references therein) showed that butterflies and other diurnal Lepidoptera such as burnet moths visited only ca. 20 out of ca. 170 potential nectar plants in the study area. Most preferred were purple and/or yellow capitula of Compositae and Dipsacaceae, with white capitula being preferentially visited by a few species (e.g. *Erebia melampus* or *Heodes virgaureae*). Furthermore, flower preferences of single species varied according to the flowers present in a particular biotope. Nectar of preferred flowers was characterized by either high volumes, moderate to high proportions of sucrose to fructose and glucose and by relatively low amino acid concentrations, or by low volumes with little sucrose but high concentrations of amino acids. The clear preference for a small, restricted number of nectar plants suggests that these nectar plants could play a particularly important role for the population dynamics of butterflies, and may thus function as keystone nectar plants. The findings of this study are also likely to apply to other areas and other biotopes and habitats (e.g. Douwes 1978, Brakefield 1982, Holbeck *et al.* 2000, Tudor *et al.* 2004).

Butterflies can also show high degrees of flower constancy (e.g. Watt *et al.* 1974, Kay 1978, Kay 1982, Erhardt & Thomas 1991). This can be important for the visited plants because it favours outcrossing. Lewis (1986) showed that memory constraints favour flower constancy in *Pieris rapae*. However, butterflies rapidly learn to associate a sugar reward with colour (Weiss 2001 and references therein). In summary, factors responsible for different flower visitation patterns and flower preferences of butterflies include innate colour preferences, learning, proboscis length, body mass and wing loading (i.e. a measure of body mass per wing area: for details see Corbet 2000), corolla tube length of flowers, flower colour and floral scent, nectar quality and quantity, and energy requirements and reproductive needs (Watt *et al.* 1974, Erhardt 1991, Porter *et al.* 1992). The ability of certain butterflies to dilute highly concentrated nectar with saliva (e.g. *Erebia* species: A. Erhardt pers. obs.) is another important factor for the different flower preferences of butterflies. Apart from these proximate causes, spatial factors clearly influence flower visitation patterns of butterflies (see below). The range and relative abundances of flower species available for exploitation vary over the geographical and ecological range of a particular butterfly species, and different flowers will be used according to geographical and ecological conditions, pointing to the possibility of geographical and ecological vicariants of keystone nectar plants for butterflies. For example, bramble (*Rubus* sp.) may play such a key role as nectar source in agricultural landscapes of Britain (Dover 1996, Dover & Sparks 2000, Dover *et al.* 2000), although *Rubus* flowers are certainly not adapted to and dependent on butterfly pollination (see below).

Since nectar is the resource butterflies get from the flowers they visit, its quality is likely to play a key role for