Meeting Report

Butterflies on the move

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The Fourth International Conference on the Biology of Butterflies and the Fragland Symposium were held at Leeuwenhorst, The Netherlands, from 23–28 March 2002.

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If biologists had to select model organisms from a single taxonomic group, butterflies would be a good choice. Contributions to the international conference on the Biology of Butterflies and a satellite meeting, the Fragland Symposium, ranged from molecular phylogenetics, through evolutionary and population genetics to behavioural, population and community ecology. Within this diversity, however, some clear themes emerged. In particular, many participants discussed the behavioural, ecological and evolutionary responses of butterflies to changes in their environment caused by recent human activity.

Responses to regional warming: from patterns to mechanisms

Butterflies provide some of the strongest evidence for the ecological effects of recent climate change [1,2]: species are flying earlier in the year (David Roy, Centre for Ecology and Hydrology, Monks Wood, UK), and are shifting their geographical ranges northwards in the Northern Hemisphere [3,4]. The close association between butterflies and the thermal environment makes them particularly sensitive to climate change, and also allows clear predictions to be made regarding their future distributions (Jane Hill, University of York, UK). Climate response models predict that, by the end of this century, marked northwards expansions in the ranges of British butterflies will be balanced by retractions in the south of their ranges, a trend that is already evident [4]. Species that currently have a northern distribution might be unable to move northwards, as their zone of climatic suitability shifts into the Arctic Ocean.

Camille Parmesan (University of Texas, TX, USA) addressed the important issue of causation: what are the mechanisms underlying recent changes in butterfly phenology and distribution? In the mountains of the western USA, extreme El Niño/Southern Oscillation (ENSO) events generate climatic conditions that could be normal in another 20 years. Such events provide 'natural experiments', which might allow the mechanisms underlying the biological effects of climate change to be identified. At high elevations, *Euphydryas editha* fared well during the last ENSO: increased accumulation of packed snow over the winter delayed larval activity in the spring, and adult emergence coincided with optimum mid-summer weather conditions. At lower elevations, the butterfly fared much more poorly, with both El Niño and its opposite, La Niña, events leading to high mortality of post-hibernation larvae. These population-level effects are consistent with the elevational pattern of extinctions in this species over the past century [3].

Over time, such ecological effects of climate change might drive and become coupled with (perhaps unpredictable) evolutionary effects. In the UK, *Hesperia comma* is now breeding in habitats that would have been too cool only 20 years ago, whereas *Aricia agestis* has 'jumped' gaps in the distribution of its traditional host plant, *Helianthemum chamaecistus*, by exploiting an alternative plant, *Geranium molle*, as it has expanded northwards (Chris Thomas and Robert Wilson, University of Leeds, UK). Female *A. agestis* in the more recently colonized localities show a clear preference for the novel plant, regardless of the most abundant host in their current environment [5]. Range expansion in these and other species might be initiated by climate, but once expansion is underway, evolutionary changes in habitat requirements, dispersal ability, and other traits could occur. For example, Marko Nieminen (University of Helsinki, Finland) has found that female *Melitaea cinxia* from newly established populations are more dispersive than are those from older populations.

The ability of species to respond to the changing climate depends on the availability of suitable habitat, which, for many butterflies in Europe and North America, now has a highly fragmented distribution. Comparison of distribution maps in *The Millennium Atlas of Butterflies in Britain and Ireland* [6] with those from an earlier survey in the 1970s provides some unsettling results. Richard Fox and Martin Warren (Butterfly Conservation, UK) described how 93% of habitat-specialist butterflies have declined in their distribution over this period, compared with only 50% of more mobile species that are typical of the wider countryside [7]. These results reinforce the need for landscape-level approaches to conservation of butterflies and other taxa.

Butterfly metapopulations: genes, behaviour and persistence

The Fragland Symposium focused on the work of a Europe-wide network of collaborators led by Ilkka Hanski (University of Helsinki) who have used empirical studies and associated modelling to address the genetic, evolutionary, population and conservation consequences of habitat fragmentation. Hanski described the development of the concept of 'metapopulation capacity', a measure that captures the influence of any particular patch of habitat on the persistence of a metapopulation and has clear implications for guiding conservation decisions. The value of a fragment depends on both the properties of the landscape in which it is embedded, but also on species-specific characteristics: rare species, close to the extinction threshold in a particular landscape, show the greatest variance in the value of particular fragments.

Compared with demographic effects, the genetic and evolutionary implications of habitat fragmentation have received rather little attention. Ilik Saccheri (University of Liverpool, UK) and Mathieu Joron (University of Leiden, The Netherlands) used *Bicyclus anynana,* rapidly becoming the butterfly biologist's equivalent of *Drosophila,* to investigate some of the genetic implications of immigration on small populations. Both

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heterosis and increased mating success of immigrants contribute to the genetic rescue of small, inbred populations, and might be frequent processes in fragmented populations.

Several contributors made the link between individual behavioural decisions, and population- and metapopulation-level processes. For example, Larissa Conradt (University of Leeds) investigated the ability of displaced butterflies to locate patches of habitat. In contrast to the random movement typically assumed in metapopulation models, Conradt's data indicate that *Maniola jurtina* butterflies use a systematic strategy to locate habitat, involving repeated forays or loops of increasing size from the starting point [8]. Simulations by Conradt and by Simone Heinz (UFZ – Centre for Environmental Research, Leipzig-Halle, Germany) illustrate the implications of this and other nonrandom dispersal patterns for the probability of individuals transferring between patches. Incorporating more realistic movement behaviour into models should lead to more accurate predictions about the ability of species to maintain and shift their distributions in an increasingly fragmented – and warmer – world.

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