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Jeremy Thomas, David Simcox and Sarah Meredith

Female Large Blue at Daneway Banks, July 2019.

David Simcox

The reintroduction of the Large Blue butterfly was the subject of the very first article published in *British Wildlife*, in October 1989. Three decades on, we are delighted to receive an update from Jeremy Thomas, the author of the original piece, along with David Simcox and Sarah Meredith, who explain how this beautiful insect has fared during the intervening years.

In two early articles in British Wildlife, we described our tentative first steps towards re-establishing the Large Blue Maculinea arion in Britain following its national extinction in 1979, and some encouraging progress made over the next decade (Thomas 1989, 1999). Success, in those days, was tenuous and far from ensured; not that we expected an easy ride. Although many had tried, no one had previously turned the fortunes of a declining butterfly, and the Large Blue was the most challenging of all the European species to conserve owing to its complex life cycle (Figure 1), which involves the caterpillar feeding on the flowers of Wild Thyme Thymus polytrichus for the first two to three weeks of its life, before it drops to the ground, where it is found by and carried into the nests of red ants of the genus *Myrmica*. There it lives for a further 10–11 months, feeding on the ants' brood and acquiring 99% of its ultimate body weight.

A remarkable life cycle

Following research in the 1970s (Thomas 1980, 2002; Thomas et al. 1989), we knew that Large Blue caterpillars were adopted indiscriminately by foragers of up to five species of Myrmica ants, which encountered them settled beneath plants of Wild Thyme, but that they survived to adulthood only with Myrmica sabuleti, whose more discerning nurse workers (usually) nurtured them. We later found that the caterpillar achieves this by secreting a cocktail of hydrocarbons that closely mimics the specific recognition pheromones of its host

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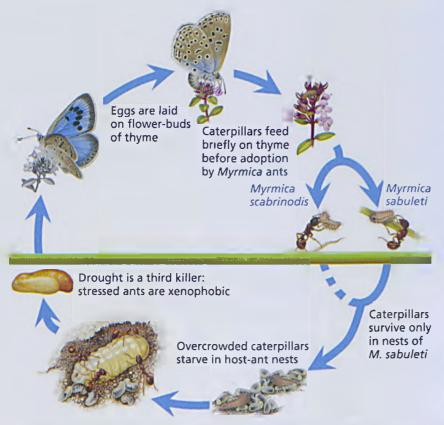


Figure 1. Life cycle of the Large Blue, based on Thomas et al. (2009). Images Richard Lewington

species. Once accepted by colony members as a nest-mate, both the caterpillar and the chrysalis elevate their status within their hosts' society by making acoustic signals that mimic the distinctive calls of a *Myrmica* queen – the most cosseted and protected individual in the whole nest (Barbero *et al.* 2009; Thomas *et al.* 2013).

Nevertheless, many caterpillars die even in the nests of *Myrmica sabuleti*, chiefly for three reasons (Thomas *et al.* 2009): (i) overcrowding and starvation when all the ant grubs have been consumed, for few *M. sabuleti* nests can support more than a single caterpillar; (ii) in nests that contain a vigorous young queen, the worker ants are stimulated to kill apparent rivals, including the mimetic Large Blue caterpillars; (iii) during periods of severe drought, when food is limited, the starving workers become more discriminating and turn xenophobic – no longer tolerant of imperfections in the chemical subterfuge of their guests, they detect, kill and eat the Large Blue caterpillars, notwithstanding their ability to 'sing' for protection.

It follows that high densities of *M. sabuleti* must coexist with flowering thyme for a site to support a colony of Large Blues, and, for a large population, there should ideally be one to three nests per square metre over at least 4ha of 'unimproved' grassland.

To achieve this, the steep hillsides that traditionally supported the butterfly needed grazing down to a short sward - on average below 1.4cm tall - during spring and autumn, allowing the sun to warm the soil sufficiently for this heat-loving ant to rear its brood during the cooler periods of their growth. Greater latitude exists under the warming climate of the past 20 years, but the niche is nevertheless still a narrow one: peak ant numbers now develop in swards that average 2.1cm or shorter and, importantly, breeding is no longer restricted to warm south-facing slopes, but can extend onto flatter terrain (Thomas et al. 2009). Sadly, this knowledge came just too late to save the last UK colony from extinction, after a century that

saw the steady abandonment of historical Large Blue sites as being no longer economic to graze (Thomas 1980, 1989). Nor were wardens prepared to crop nature reserves so heavily without good reason. It is hard to remember in these days of agrienvironment schemes just how overgrown - and bereft - our 'unimproved' lowland hillsides had become. The Cotswold downlands, for example, were almost universally dominated by a thatch of knee-high Brachypodium, and wider surveys of 109 sites for Lulworth Skipper Thymelicus acteon, Adonis Blue Lysandra bellargus and Large Blue in south-west England showed an average sward height of 14.2cm in the 1970s, whereas in the current century it is 10cm shorter (Thomas et al. 2015).

The first introductions

In early issues of *British Wildlife*, we described in some detail how a consortium of scientific and conservation bodies (see Acknowledgements), founded in 1963 to conserve the Large Blue and still delivering the project, sought to restore Large Blue habitat with the aim of re-establishing the butterfly in Britain. We also described the odyssey of searching in Europe for a near-identical race of Large Blue that was physiologically suited

to survive under UK climates and with English ants. This was difficult, for the butterfly was extinct across much of northern Europe for the same reasons as in the UK. We eventually found a potential donor colony on the beautiful Stora Alvaret limestones of Oland, in south-east Sweden, which the authorities generously allowed us to use. We made three collecting trips, painstakingly rearing single eggs (since young caterpillars are cannibalistic) for release as caterpillars weighing 1-2mg into M. sabuleti territories - this remains the most reliable method of establishing a new colony. The first release, in 1983, was a trial in which we distributed 93 caterpillars across the National Trust's 'Site X' on Dartmoor, which had supported the UK's last native colony. This was immediately successful and led to a second, larger release of larvae in 1986, to raise the numbers to safer levels and to increase genetic diversity. The final collecting trip in Sweden, in 1992, produced 581 caterpillars, which we introduced to the Somerset Wildlife Trust's Green Down nature reserve (281 caterpillars), and to Rough Banks, in the Cotswolds (300 caterpillars). Although they failed to establish on Rough Banks, for reasons which we now understand, the introduction to Green Down was a success. Indeed, during the present century Green Down has supported the largest known population of this globally Endangered species in Europe, and perhaps the world. All current UK populations stem from that single introduction.

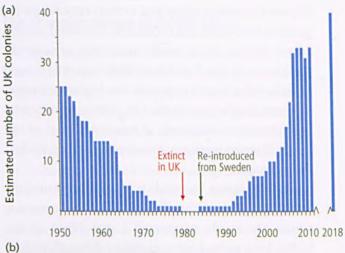
Thanks to sterling efforts by site-managers to restore, and then maintain, what by now was confirmed as optimum habitat on a growing number of former and potential sites, we were able to write in the second article for *British Wildlife* (Thomas 1999): 'the re-establishment project has been much expanded, so much so that the Large Blue flew on eight sites in 1999 and in four of the six regions from which it was formerly known. Some of the new populations are exceptionally large for this species, some are weak and precarious, and two involve very recent trials. Overall, we are perhaps halfway towards fulfilling the recovery programme planned for this butterfly...'

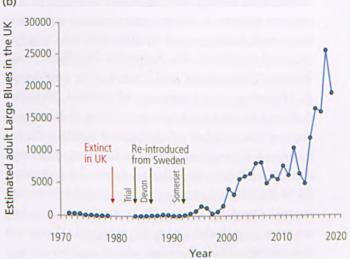
Setbacks and success

Twenty years on, we are pleased to report that the Large Blue bred on 40 UK sites in 2018, and its populations combined have increased from about

1,500 adults in 1999 to more than 19,000 in 2019 (Figure 2). A record count (to date) of more than 25,000 adult Large Blues emerged over eight weeks in the unforgettable summer of 2018, thanks to textbook grazing achieved by the National Trust and Wildlife Trusts of Somerset and Gloucestershire on the 'big three' sites of Collard Hill, Green Down and Daneway Banks, and assisted by near-perfect weather during the preceding year. The dip in 2019 was caused by overcrowding of caterpillars in ant nests - on Green Down, for example, more than 16 eggs had been laid per square metre - and, in Somerset, by the impact of a severe summer drought. This is all very encouraging, but a word of caution is needed: perhaps only a third of current colonies are stand-alone populations that would, we are confident, persist more or less indefinitely given suitable land management. The rest may depend to some extent on immigrants from the core populations, and some are undoubtedly satellite

Figure 2. The number of Large Blue colonies in the UK, 1950–2018 (a) (updated from Thomas et al. 2009), and the estimated number of Large Blue adults flying in the UK, 1971–2019 (b).





colonies. Nor has the seemingly smooth progress shown in Figure 2 been without its setbacks. Let us mention two disappointments before describing happier developments.

It was perhaps disingenuous to claim, in 1999, that the Large Blue flew 'in four of the six regions from which it was formerly known'. Two of those regions, the Atlantic coast of Devon and Cornwall and the Cotswolds, involved uncertain trials that faltered after two to four generations. And, sadly, it proved too costly for site-managers to support a population on the acid shales on the edge of Dartmoor owing to the need for intensive input, which involved annual swaling of gorse Ulex as well as appropriate grazing. Besides, these thinsoiled sites were intrinsically less suited to support high densities of Large Blues even in the best of years, and they were particularly susceptible to (increasingly frequent) summer droughts. With a heavy heart, these colonies were abandoned, and 22 generations after its reintroduction, the Large Blue died out on Dartmoor. Achieving continuity of suitable management on the Atlantic coastal sites has also proved elusive, owing to the major work required to reduce scrub and to their remoteness for graziers who were not necessarily stationed nearby. Nevertheless, these acidic maritime grasslands, together with the Bolt Head-Bolt Tail valleys west of Salcombe, once supported the highest densities of Large Blue known in the UK. Although resources are currently inadequate, it remains a goal of the Large Blue consortium to restore and repopulate these regions.

The succession to scrub is slower on limestone grassland. Hence the Polden Hills in Somerset, which previously supported Large Blues in the 1840s, have proved more tractable, although seldom easy, to restore. Crucially, the partners who own, lease and manage sites in this region - notably Natural England, the Somerset Wildlife Trust, National Trust, J&F Clark Trust, Centre for Ecology & Hydrology, the University of Oxford, Network Rail and Millfield School - have been unstinting in their enthusiasm and reliability, and highly skilled in delivering the evolving evidence-based management recommendations supplied to them. Consequently, 34 of the UK's current Large Blue breeding sites are located along this seven-mile escarpment, including ten core populations of quite exceptional size for this species. The others are either smaller or still

developing, and some may always be minor satellites, not occupied in every year, but nonetheless important in that they provide stepping stones for dispersal between the main populations.

Collard Hill, owned and managed by the National Trust, supports the second largest colony in Somerset and is a major asset in other respects. Alone in this region, it has sufficient parking arrangements for the hundreds of naturalists who flock there each summer to watch and photograph the Large Blue. The National Trust also installs a ranger each season to welcome and inform visitors, and to post daily updates to the popular blog (https://ntlargeblue.wordpress.com). Between and beyond Collard and Green Down lies a string of current and potential sites in various stages of restoration and occupancy. Several were failing conifer plantations, planted on these unpromising soils in the 1950s, for which four partners won National Lottery funding to restore to grassland. The aim was by no means solely to encourage the Large Blue, but it was expected that much suitable habitat would develop as a result, as indeed has proved to be the case.

Perhaps our most unlikely sites are four Network Rail properties (all strictly prohibited to visitors) that support six distinct colonies beside the main line from Paddington to Taunton. The first of these was colonised – ironically on ground for which no management plan existed – in 1995, just three years after the introduction at Green Down. These sites are much easier to maintain because their unnaturally steep sheltered sides create a microclimate more characteristic of central-southern Europe, where

Myrmica sabuleti tending a 1mg Large Blue caterpillar prior to adoption during the 2010 reintroduction to Daneway Banks. David Simcox







Female Large Blues laying eggs on two neighbouring sites in Somerset. Marjoram is used as the foodplant at one (a) owing to a hot microclimate and taller sward, while on a typical UK downland site the eggs are laid on Wild Thyme (b). In both cases, females lay only on tight flower-buds. David Simcox

spring-autumn temperatures are so warm that Myrmica sabuleti nests in taller turf, half-shaded from the sun's rays. The same niche is occupied on Somerset's railway banks where, except in one site, the butterflies lay their eggs on the tall flowerheads of Marjoram Origanum officinale, the swards being too tall for Wild Thyme. Being Victorian artefacts, these cuttings and embankments are less stable than natural downland, and two of them needed major construction works in 2004 and 2006. These provided an exciting opportunity: the ultimate test of creating our definition of Large Blue habitat 'from scratch', beginning in both cases with bare limestone ballast. The fundamental structures were, of course, designed by Network Rail engineers, but they were happy for us to determine the surface layer, and in one case to devise a micro-topography of multiple aspects that has provided a spectrum of micro-climates that buffer the impacts of extreme drought, or cold wet years, on ants, butterflies and other wildlife. Instead of the conventional thick layer of topsoil, crafted to billiard-tabletop smoothness and sown with robust cultivars of grass, we substituted a thin layer of rough calcareous subsoil, sown with a species-rich seed mix of calcicoles of local provenance, including high densities of Marjoram, which was hydraulically sprayed on to the new slopes. Myrmica sabuleti, though swift to desert an unsuitable site, is equally quick to colonise one that is favourable, and high densities developed within six years. As well as containing an exciting range of other wildlife, both sites today support viable populations of Large Blue, one quite small but the other the fifth largest in the UK in 2019. It is worth noting that the costs for Network Rail of both constructions were lower than if topsoil had been imported, and in one case saved an estimated £250,000.

The partnership's work in the Polden Hills is far from complete. In addition to annual habitat assessments and management advice on all sites, similar restorations of degraded grasslands, as well as habitat creation on former arable fields and failing conifer plantations, have started or are planned on extensive areas owned by the J&F Clark Trust. In addition, restorations led by Butterfly Conservation are making fine progress in the wider Poldens. Together, we plan that this hotspot for the Large Blue may support double the present number by 2040.

The changing nature of British blues

We have already noted that all current UK populations of Large Blue butterflies stem from a single introduction of 281 caterpillars from Öland made in 1992, 27 butterfly generations ago. One advantage of sourcing eggs widely across the Great Alvaret was that they were laid by different females and, we hoped, contained maximum genetic diversity. This was confirmed by Andersen et al. (2013), who found that the Somerset populations contained similar high levels of genetic diversity to the source populations, although the butterflies on Collard had differentiated from those on Green Down. Indeed, 'our' UK colonies possess four alleles that have apparently disappeared from Öland, perhaps owing to a population crash there in 1993 caused by an unprecedented drought. It has cheekily been suggested that we make a reverse translocation from Somerset to Sweden in order to restore the degraded gene pool. More seriously, the introduced butterflies have had sufficient diversity to adapt to their UK environment in two helpful ways. First, compared with the original Swedish phenotype, the British Large Blues are today spreading more quickly to recently restored sites, presumably owing

to selection for a more dispersive race as females gradually advanced by stepping-stone colonisation from one new patch to the next (Dempster 1991; Hill et al. 1999). Not that dispersal is by any means speedy: now it takes four years, on average, for the butterfly to colonise new habitat located 1km from an existing population, whereas it took six and a half years to achieve this in the 1990s. This means that we still need to make deliberate introductions to new isolated sites, despite its being time-consuming and expensive. Reliance on natural dispersal would have meant, for example, that the diligent managers of Collard Hill awaited a 50% chance of the butterfly colonising unaided within the next 52 years! Nevertheless, it is satisfying to note that nearly 90% of colonies in Somerset were founded by natural spread.

The second adaptation provided an unexpected key to success in the Cotswolds. We knew already that our early introductions direct from Sweden to former sites failed because the adult butterflies emerged too late to synchronise with flower-bud production of thyme. That restricted the females to laying eggs on the few late-flowering plants that grew in the coolest parts of the sites, the only places where M. sabuleti was absent (Thomas 2017). We had moved them an isotherm too far. In Somerset, where spring and summer local climates were around 1.5°C cooler than the source sites in Sweden, the synchrony was imperfect but adequate. In the Cotswolds, where temperatures were a further half-degree cooler, it was not. Just 13% of females emerging on Rough Banks and Barnsley Warren coincided with the brief window when the thyme flowers were in the tight buds acceptable to the female butterfly.

Thus, 20 years ago, we wrote of a trial introduction to a third, fractionally warmer Cotswold site, Daneway Banks, that 'This should tell us whether any Gloucestershire site is suitable for this race of butterfly under the current climate. If this should fail, the search will begin for a better-adapted race of Large Blue on the Continent' (Thomas 1999). I hat trial did succeed – at least until bovine TB prevented grazing and the colony died out – but not for the reason that we expected. During the intervening years, the imperfect but adequate synchrony between thyme flowering and the flight period of the butterflies in Somerset led to strong selection for earlier emergences. After 12





(a) Spraying a seed mix of local provenance on a new railway construction designed to support the Large Blue. (b) Habitat created from scratch in 2004 on an embankment that now supports the fifth largest UK population of Large Blue. Jeremy Thomas

generations, Large Blues were emerging 10–12 days earlier after equivalent weather, and their flight period spanned the exact dates of peak flower-bud production. When this strain was translocated to Daneway, the emergence dates were earlier there as well, and almost exactly on cue with the extinct Cotswold race.

To complicate the story further, it soon became apparent that, while the early-emerging race was evolving on Green Down, a late-emerging race later than the original Swedish introduction - was evolving simultaneously on our railway cuttings, in response to the later flowering of Marjoram. Armed with this knowledge, we made a second introduction at Daneway Banks in 2010. By that time this exquisite grassland was well grazed by Welsh mountain ponies and Norfolk longhorn sheep, and its future was soon secured when it was bought jointly by the Gloucestershire Wildlife Trust and the Royal Entomological Society (RES) (Thomas 2017). Thanks to a grazing regime that enabled Myrmica sabuleti to co-occur with Marjoram as well as with Wild Thyme, we decided to introduce both late-emerging and early-emerging

'races' of Large Blue: thyme-using individuals sourced from Green Down and Collard Hill, and Marjoram-using caterpillars from one of the railway sites. This not only was successful, but also resulted in a double peak of butterflies in the first six years, each perfectly attuned to its respective foodplant. The use of two plants roughly doubled the breeding area for Large Blues on Daneway, and the population, now in its tenth generation, quickly grew to rival those on Green Down and Collard Hill.

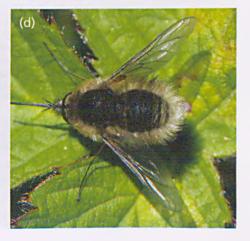
It was a great relief to have cracked the Cotswolds, 18 years after our first attempts. Today, the key owners and managers of sites in this region – Natural England, the National Trust, Gloucestershire Wildlife Trust and the RES – are embarked on a programme to re-establish three meta-populations of Large Blue on multiple former sites across its historical Cotswold range. The essential advisory work, habitat analyses and new introductions are funded by these organisations, along with a major grant from the Prince of Wales'

Collateral gains from 'Large Blue management' in acid grassland exemplified by the National Trust's Dartmoor Sites X, Y and W. (a) Pale Heath Violet, (b) Pearl-bordered Fritillary, (c) High Brown Fritillary, and (d) Western Beefly. Jeremy Thomas (a, b); David Simcox (a, d); Peter Eeles (c)









Charitable Foundation and Butterfly Conservation's Biffa and 'Back-from-the-Brink' lottery' award. In 2017–19, we made new introductions to two potentially major sites. One of these, Painswick Beacon, is a classic site for this species, and promising emergences have already been recorded.

An umbrella species

Management for the Large Blue has proved to be beneficial for many other prized wildlife species. The approach in essence involves turf being close-cropped and lightly scarred between autumn and spring in order to create a short, open sward that is then left fallow during May to mid-August, encouraging flowers to bloom and seed, and insects to breed, on the infertile soils. On several sites, a mosaic of smaller sub-areas is also being rotated or maintained as mid-successional to taller swards with mixed-age scrub to support, among much else, such rarities as the Liquorice Piercer moth *Grapholita pallifrontana*, the Duke of Burgundy butterfly *Hamearis lucina*, the Nightingale *Luscinia*

megarhynchos and the Woodlark Lullula arborea. Meanwhile, in the extensive shorter grassland, there has been a resurgence of warmth-loving species, most of which are in steep decline elsewhere. On the acid shales of Dartmoor (Thomas 1999), for example, there were roughly hundred-fold increases in two species of violet Viola, including the rare Pale Dog Violet V. lactea, the seeds of which possess an elaiosome (a fleshy structure) that is particularly attractive to Myrmica ants (Randle et al. 2005). At the height of management of sites X and Y, roughly one million of these beautiful plants were in bloom. These violets in turn supported four species of fritillary - Pearlbordered Boloria euphrosyne, Small Pearl-bordered B. selene, High Brown Argynnis adippe and Dark Green Fritillaries A. aglaja - each of whose populations increased roughly

tenfold over the 40 years during which these sites were under management: over the same time, most other colonies of the first three species went extinct. Other notable increases on sites X, Y and W included populations of the Western Beefly Bombylius canescens, Hornet Robberfly Asilus crabroniformis and Lesser Cockroach Ectobius panzeri.

Similar collateral gains occurred on the limestone sites in Somerset and the Cotswolds. As well as striking rises in populations of common plants such as Cowslip Primula veris, Rock Rose Helianthemum nummularium and Wild Thyme, there were also substantial increases in Cut-leaved Germander Teucrium botrys (at one of about six UK colonies), Cut-leaved Self-heal Prunella laciniata (three of its c. 30 colonies are thriving alongside Large Blues) and several orchids, including the Green-winged Anacamptis morio, Frog Dactylorhiza viridis and Fly Orchids Ophrys insectifera. In addition, increases were recorded for numerous red-listed insects, including the strangely beautiful Rugged Oil Beetle Meloe rugosus, whose larvae feed as kleptoparasites in the pollen chambers of the abundant solitary bees that have multiplied on these slopes (Thomas et al. 2019).

The Large Blue butterfly, therefore, acts as a protective umbrella for a diversity of other species that either interact directly with ants or inhabit similar warm, early-successional niches within British grassland. There is little doubt that it is these collateral gains that have encouraged the conservation bodies of the Large Blue partnership to place so much effort, expertise, resources, goodwill and sheer enthusiasm into the restorations. Long may it continue, for there is much still to be done: we hope to expand the Large Blue in the Poldens, establish meta-populations of colonies on former sites across the Cotswolds, and in due course repopulate the Atlantic coastal valleys between Boscastle and Hartland, and the maritime grasslands west of Salcombe. But, for now, the Large Blue is flying in Britain in the highest numbers for at least 100 years, and its future looks more secure than at any point since its heyday in the 19th century.

Acknowledgements

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Jeremy Thomas chairs the Joint Committee for the Re-establishment of the Large Blue Butterfly, and was the Project Officer from 1972 to 1999. David Simcox was Deputy Project Officer from 1982 to 1999 and has been Project Officer since 1999. Sarah Meredith has been Deputy Project Officer since 2012.