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Article (Accepted Version)

Ecology and conservation of the British Swallowtail butterfly, *Papilio machaon britannicus*: old questions, new challenges and potential opportunities

N. Mark Collins[1], Patrick J. Barkham[2], Michael Blencowe[3], Andrew Brazil[4], Andrea Kelly[5], Sara Oldfield[6], Tim Strudwick[7], Richard I. Vane-Wright[8] and Alan J.A. Stewart[9]

[1] Swallowtail and Birdwing Butterfly Trust, c/o Hines Harvey Woods, Queens Head House, The Street, Acle, Norwich NR13 3DY, UK, [2]c/o The Guardian, 90 York Way, London, N1 9GU, UK; [3]c/o Sussex Wildlife Trust, Woods Mill, Old Shoreham Road, Henfield, West Sussex, BN5 9SD, UK; [4]19 Beeching Road, Norwich, Norfolk NR1 2LE, UK; [5]Broads Authority, Yare House, 62-64 Thorpe Road, Norwich NR1 1RY, UK; [6] 5 Marshall Road, Cambridge CB1 7TY, UK; [7] RSPB Strumpshaw Fen, Low Road, Strumpshaw, Norwich NR13 4HS, UK; [8]Department of Life Sciences, Natural History Museum, London SW7 5BD, U.K. & Durrell Institute of Conservation and Ecology (DICE), University of Kent, Canterbury CT2 7NR, UK; [9] School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK.

* Address for correspondence: Dr N.M. Collins, Chairman, Swallowtail and Birdwing Butterfly Trust, c/o Hines, Harvey, Woods, Queens Head House, The Street, Acle, Norwich NR13 3DY; (mark@sbbt.org.uk)

Abstract

1. The British Swallowtail, *Papilio machaon britannicus*, is an iconic flagship for its unique but now restricted and fragmented fenland ecosystem in the UK's Norfolk Broads.
2. Occurrence in 1 km^2 recording squares fell by 56% over the period 1974–2014 and by 13% 2005–14, but the breeding populations, mainly confined to reserves, have increased in size.
3. Climate change-induced sea-level rise and consequent seawater incursion into the Norfolk Broads represent a significant existential threat to the butterfly.
4. Translocation to more secure fenland sites is recommended; several are being restored or recreated through stakeholder partnerships in East Anglia and Somerset.
5. Well-researched introduction and management of the foodplant, Milk-parsley, is essential for such translocations to succeed.
6. A better understanding is needed of the genetic structuring of the British Swallowtail populations using modern sequencing technologies, in particular to elucidate the significance of gene flow in relation to the viability of introductions to small or isolated sites.
7. In a species in which hybridisation is commonplace across the Holarctic, the continued influx and future spread in Britain of the continental subspecies *Papilio machaon gorganus* may present a threat to the genetic integrity of subspecies *britannicus*, despite their differences in habitat and larval foodplants.

Key words: Swallowtail; Norfolk Broads; Milk-parsley; *Peucedanum palustre*; fen; sea-level rise; hybridisation; *Papilio machaon;* reintroduction; translocation

Running title: Conservation of the British Swallowtail

Introduction

Despite its iconic status as Britain's largest resident, native and endemic butterfly, the British Swallowtail, *Papilio machaon britannicus* Seitz, 1907, has received limited research attention or commentary in the literature in the past quarter century, notwithstanding important changes in its environment. Accordingly, on 27th June 2018, 50 participants representing 25 organisations convened by the Swallowtail and Birdwing Butterfly Trust and with the support of the Royal Entomological Society, met at the Ted Ellis Trust's nature reserve at Wheatfen in Norfolk, UK, to review the current conservation status of swallowtails in Britain and to draw together their concerns and recommendations (Harrington, 2018).

The taxonomy of *Papilio machaon* L., the polytypic north-temperate species to which the British subspecies *britannicus* belongs, is complex and continues to change with new, notably molecular research. While the British Swallowtail today is isolated and has a narrow distribution, it is a member of a Holarctic ring of more than 20 subspecies distributed across the northern Palaearctic from Britain to northern Japan and throughout central and western North America. It is often assumed that *P. m. britannicus* is most closely related to the two western European subspecies, *P. m. machaon* L. from Scandinavia and, especially, *P. m. gorganus* Fruhstorfer from France. This is, however, an assumption which needs to be re-investigated by molecular methods. Compared with *P. m. gorganus*, the phenotype of the British Swallowtail is slightly smaller with a darker overall appearance, deeper yellow ground colour, broader hind wings with shorter tails and broader, darker submarginal bands. However, considerable variability exists between individuals within these subspecies, making identification based solely on adult external appearance problematic.

After providing an updated conservation assessment and some relevant background on the ecology of the Swallowtail and its foodplant Milk-parsley (*Peucedanum* (=*Thyselium*) *palustre* (L.) Moench), we outline the current threats and propose a proactive approach to securing a sustainable future for this spectacular and nationally important butterfly.

Conservation assessment

As a result of difficulties in differentiating between subspecies, unravelling an historical baseline for the distribution of *P. m. britannicus* upon which to base a reliable conservation assessment is complicated. Early recorders often did not distinguish *britannicus* from *gorganus*, which periodically migrates into southern England, especially in hot summers. For this reason, early records of putative *britannicus* need to be corroborated by examination of museum specimens. Such evidence suggests that *britannicus* once occurred widely in the East Anglian fenlands and broadlands and very possibly as far afield as the Thames basin, Somerset Levels (but not into the 19th century), Warwickshire and even Yorkshire. One of the earliest recorders, James Petiver (1717:1) noted that the Swallowtail "has been caught about *London* and divers *Counties in England*, yet rarely."

Over several centuries, widespread drainage and agricultural conversion of the fens of Lincolnshire, Cambridgeshire, Suffolk, Norfolk and elsewhere restricted the butterfly's range. In the last decade or so it has been confined to the Norfolk Broads alone (Figure 1). As a result, the British Swallowtail is today a protected species under Schedule 5, Section 9 of the Wildlife & Countryside Act, 1981, affording it protection from intentional killing, possession or sale of specimens, or disturbance of its habitat (notwithstanding the fact that its survival now depends upon prevention of serial succession by scrub clearance).

The UK Red Data Book for insects listed the British Swallowtail as Vulnerable (Shirt, 1987) but the only Species Action Plan for the subspecies, published in 1995, described it as "under no immediate threat" and listed it as only a medium priority for conservation (Barnett & Warren, 1995). Asher *et al*. (2001), in the *Millennium Atlas*, also expressed little concern and some later reports in the press (e.g. Roberts, 2010) even painted a picture of strong recovery. In contrast, in 2006 *P. m. britannicus* was considered a Species of Conservation Concern (Fox *et al*., 2006). In 2010 Fox *et al*. concluded that it was Near Threatened (NT) on the basis of its restricted area of occupancy (fenland in East

Anglia, UK) and a continued decline in the area, extent or quality of habitat available to it as a result of succession from fen to unsuitable ecotypes (partly due to the decline in demand for reed for thatching and animal bedding) and continuing conversion to agriculture.

A more recent assessment of the butterfly's status, combining data from the *Butterflies for the New Millennium* recording scheme facilitated by the Biological Records Centre since the 1970s and the *UK Butterfly Monitoring Scheme* since 1976, goes some way towards explaining these inconsistencies. Fox *et al*. (2015) describe a nuanced picture comprising a significant and welcome 88% increase in total population size over a 40-year period up to 2014 but, at the same time, a concerning 56% decline in the occupancy of 1 km squares. In effect, the butterfly has prospered numerically, but within a much smaller range.

Today, few sites are managed specifically for the British Swallowtail, Catfield Fen in Norfolk being an exception (Butterfly Conservation, undated). Nevertheless, targeted management for the species in the wider context of the entire plant, vertebrate and invertebrate community has undoubtedly been responsible for the great improvement in its population level in Broads reserves in recent years. As a result of focused scrub clearance and water management by the Broads Authority, Natural England, Norfolk Wildlife Trust, the RSPB, Butterfly Conservation, the Ted Ellis Trust and many other individuals and organisations, the Swallowtail population in the Norfolk Broads is currently stable, albeit within a very narrow (and vulnerable) geographic range.

This unusual situation reflects the operation of two opposing factors: considerable recent success in managing the habitat for this species at its remaining protected strongholds in the Norfolk Broads, but at the same time a serious decline in the number of suitable sites available elsewhere. In effect, the wider countryside has become increasingly inhospitable to the Swallowtail, which cannot of its own accord reach suitable unoccupied habitat that still survives or is being recreated. The risk of extinction has risen as there are now no alternative refuges in the event of an environmental shock to existing sites (such as a saline tidal surge), or a severe downturn in the resources available for fenland reserve management, in addition to the more usual threats to rare species.

Given the perilous state of many other species of butterfly in Britain, it is reasonable to ask why the allocation of scarce resources to the conservation of the Swallowtail might merit re-examination. We contend that the threats that have recently emerged or assumed greater potency in the last 25 years, all ultimately traceable to the effects of a changing climate, represent a much greater risk than has so far been recognised. Unless these issues are addressed with some determination, the British Swallowtail, arguably one of our finest butterfly species, faces extinction in Britain.

Ecology of the British Swallowtail

An understanding of the ecology of the Swallowtail and of its foodplant, Milk-parsley, is fundamental to any plan of action. Dempster (1995) provided the most recent full account of the British Swallowtail's ecology and conservation, while Nicholls & James (1996) gave detailed reports on behavioural ecology. Building on those reviews, it is instructive to ask why the many subspecies of *Papilio machaon*, whose morphological characteristics are so difficult to distinguish, should be considered separately.

Across the Old World, *Papilio machaon* is generally an oligophagous species utilising a wide variety of Apiaceae. In Sweden, for example, *P.m. machaon* uses three different species according to habitat (Wiklund, 1974; Wiklund & Friberg, 2008). However, at the subspecific level larval food requirements can differ widely and be much more narrowly constrained. In France, for example, *gorganus* larvae feed on various widely distributed species of Apiaceae and adults disperse long distances across a variety of different habitats, but in Norfolk *britannicus* is a narrow specialist on its foodplant Milk-parsley, *Peucedanum palustre*, and occurs only in tall-herb fen (classified in National Vegetation Classification terms as community S24: *Phragmites australis – Peucedanum palustre* fen; Rodwell, 1995). Moreover, *britannicus*, unlike *gorganus*, usually does not manage two full annual generations. Those larvae that reach sufficient size before a critical point in day-length pupate and emerge in the same year (bivoltine) but the majority that do not, enter diapause and emerge next spring (univoltine) (Dempster *et al*, 1976, Dempster, 1995). In this context we note that *P. m. machaon* in Fennoscandia is also normally univoltine (Wiklund, 1974), with only an occasional second generation (Henriken & Kreutzer, 1982). Despite the fact that *P. m. britannicus* and its continental conspecifics *P. m. gorganus* and *P. m. machaon* share a very similar appearance, it is clear that this hides significant ecological and behavioural differences.

Although there are informal reports of British Swallowtail larvae being found on wild plants other than Milk-parsley, no publications have reported successful pupation and emergence. In Swallowtail habitat such as at Wheatfen Reserve on Norfolk's River Yare, a dozen species of Apiaceae may be found, but none of them has been observed to be used by the Swallowtail except Milk-parsley (W. Fitch, pers. comm.). Surprisingly, however, it is generally not difficult to breed the Swallowtail in captivity on other plants, especially Wild Carrot (*Daucus carota*) (Gardiner, 1963), indicating that the foodplant may not be the only factor that limits the butterfly to its precise ecological niche.

Egg-laying tends to favour the largest and most prominent plants, sometimes growing on tussocks (Nicholls & James, 1996), seemingly because they are more visually apparent to gravid females which, flying above the vegetation, approach foodplants on a horizontal trajectory (Wiklund, 1974). Females generally lay just one egg per plant, but nevertheless, several larvae of different instars are often found together on a single plant, perhaps from several females. Larvae of the first three instars are predominantly black with a yellowish saddle and are believed to be camouflaged as bird droppings, while the final two instars show the more familiar aposematic green, orange and black markings (Porter, 2010).

Pupation often takes place on stems of Common Reed, *Phragmites australis,* Great Fen-sedge, *Cladium mariscus,* or Greater Tussock-sedge, *Carex paniculata*. Pupation takes place up to 60cm above water level (Dempster *et al*., 1976) and the ameliorating effect of the standing water on the winter microclimate may be important for successful pupation. However, where the fen is tidal, such as at Wheatfen, water levels can vary by up to 30cm or more and those pupae lower down on stems are therefore presumably inundated for long periods, particularly in winter. Survivorship under such conditions has not been fully studied but, despite informal accounts of pupae surviving underwater, many must be lost. Indeed, annual climatic variations are known to have an over-riding impact on Swallowtail populations (Pollard *et al*., 1986), whose success is also influenced by avian and mammalian predators, pathogens and the rare ichneumonid parasitoid wasp *Trogus lapidator* F., (Nicholls & James, 1996; Nobes, 2008).

Ecology of the foodplant, Milk-parsley

Milk-parsley in Britain is best described as a short-lived perennial, surviving for up to five years in certain tall-herb lowland fen plant communities. It remains fairly common in the Norfolk Broads and also has a strong population in the Somerset Levels (Borsje, 2005), but is now very rarely found elsewhere (Meredith & Grubb, 1993). Its Vulnerable conservation status is based on recent population decline due to loss of habitat area and quality (Cheffings & Farrell, 2005; Stewart *et al*., 1994). In addition to the Swallowtail, its predators and parasites, Milk-parsley supports a wider food web, including an agromyzid fly *Phytomyza thysselini* Hendel, first discovered in Britain in 1983, whose larvae mine the leaves (Panter *et al*., 2011).

Much habitat for Milk-parsley was lost in the 17th, 18th and particularly 19th century due to widespread drainage and reclamation of the East Anglian and other fenlands; since then, the main change has been habitat deterioration due to serial succession and scrub invasion. The majority of sites where it survives are closely-managed nature reserves where scrub and groundwater regimes are controlled. The principal remaining threat has been altered water regimes, including water quality and flows, due to pollution and drainage of surrounding habitats for agriculture.

Much of our knowledge on the ecology of Milk-parsley derives from the account by Meredith & Grubb (1993). The species is quite easy to grow *ex situ* under greenhouse or sheltered conditions and there is every possibility of propagating plants, for example to augment existing populations. However, its occurrence in natural fen habitats is patchy for reasons that are not fully understood and more research is needed if population augmentation or introduction is to succeed. The plant produces many seeds and these are dispersed over short distances by water and wind. Long-distance dispersal to new sites, for example by birds, is probably infrequent. Germination requires damp but not flooded soil conditions and responds positively to the open habitat conditions produced by infrequent reed cutting and scrub control. Milk-parsley will not tolerate dry conditions. Historically, fen was mowed to collect reed and sedge for thatching and to collect 'marsh hay' for cattle fodder and animal bedding. Today, default fen management for conservation still includes mowing, but less frequently than in the past and with some additional grazing by cattle or ponies (McBride *et al*., 2011). Much variation in mowing practice exists in terms of timing (late summer, autumn, winter), method (brush cutter, mower, fen harvester), length of rotation cycle (4, 6, 8 years), purpose (conservation; single and double wale commercial cutting; 4-yearly sedge cutting) and whether or not the cut material is removed or burnt *in situ*. Some areas receive no mowing or other management, except periodic removal of scrub.

No experiments have focused specifically on the effects of these different forms of management on Milk-parsley, but a number of observations have been made. Dempster *et al*. (1976) indicated that a four-year cutting rotation is optimal for promoting the tall flowering plants that *P. m. britannicus* seems to prefer and which take three years or more to reach full size, whilst at the same time holding back succession and scrub invasion. However, a recent study in the Mid Yare National Nature Reserve, Norfolk provides some preliminary evidence in support of less frequent management (T. Strudwick, pers. obs.). Over an eight-year period, the mean density of Swallowtail larvae recorded in unmanaged fen was more than twice that in regularly mowed fen or grazed fen, although high annual variation meant that the differences were not statistically significant. Nevertheless, the fact that high numbers of larvae were reported only in unmanaged fen suggests that the other forms of management produced Milk-parsley plants that were often not sufficiently large to attract egg-laying Swallowtails.

Water quality is also important to Milk-parsley. In their biodiversity audit of the Broads, Panter *et al*. (2011) classify the Swallowtail amongst the 63% of Broads species that require fully freshwater conditions, i.e. freshwater with conductivity values <800 μs/cm. This response of the butterfly is presumably due to the intolerance of Milk-parsley to salinity, which is at its lowest levels in the Rivers Ant, Bure and mid-Yare, where Milk-parsley, Swallowtails and other freshwater obligates are predominantly found (Panter *et al.*, 2011). Loss of Milk-parsley communities that have been recorded in the Mid Yare NNR have coincided with elevated salinities following a series of surge tides.

Further experimental research is needed on the precise edaphic conditions and management operations that are needed to encourage germination and rapid growth of the mature, tall plants that the butterfly favours. More work is also needed on the impact of different conservation management practices on Milk-parsley populations, especially different types of mowing, scrub clearance and maintenance of water levels. Its seemingly exacting ecological requirements make Milk-parsley vulnerable to inappropriate management, for example when imposed for the benefit of other priority species. Such studies will become key to *in situ* conservation of the Swallowtail in coming years.

Ecological interactions and the implications for conservation planning

Adult *P. m. britannicus* are strong fliers (Brazil *et al.*, 2011) and are often recorded visiting gardens in search of nectar (Dempster, 1995). Males can disperse widely in search of females, particularly when population density is low in second broods. Recent sightings suggest that the most dispersed records broadly describe an arc of 30km distance from the known breeding sites (Brazil, 2018; Figure 2). The implication is that *britannicus* is unlikely naturally to colonise newly-created sites that are further afield than this, even if the foodplant is present. Unfortunately, distances from the Broads to other potentially suitable sites such as Wicken Fen (which has Milk-parsley), Lakenheath Fen and

Woodwalton Fen (which have none) are all between 80 and 100km. Large areas in the Somerset Levels, for example Shapwick Heath National Nature Reserve, have substantial Milk-parsley populations but are more than 400km away. Individual adult Swallowtails have occasionally been recorded in distant locations, but the presumption in such cases is that pupae have been transported with Norfolk reed used for thatching (Rothschild, 1975).

Moreover, progressive habitat fragmentation is believed to have reduced the ability of the butterfly to disperse and colonise new sites. Morphometric measurements of museum specimens of *britannicus* have demonstrated rapid evolutionary responses to the changes in landscape structure around both the former Wicken Fen and Norfolk Broads populations since the late nineteenth century (Dempster *et al*., 1976). Greater wing length and reduced thorax width relative to body length in more recent specimens were interpreted as adaptations for reduced mobility as populations became isolated by habitat fragmentation and destruction.

Based on allozyme and RAPD-DNA analyses, Hoole *et al*. (1999) found very limited genetic differentiation between three of the larger local populations of *britannicus* within the Broads. On this basis, they concluded that the Norfolk populations in fact comprised one large intermixing population with regular movement of individuals, and therefore gene flow, between sites. Twenty years on, this conclusion should be revisited using non-destructive modern genomic approaches. Ultra-high-throughput sequencing methods based on single nucleotide polymorphisms (e.g. RADseq; Andrews *et al*., 2016) might uncover population structuring that was missed by the previous less powerful (and less reproducible) molecular marker techniques, as Dupuis and Sperling (2016) found when examining hybridization between *P. machaon* and *P. zelicaon* in Canada. The amount of mixing between spatially separated localities will help define population boundaries in this species, which in turn will have important implications for developing future conservation strategies. Frequent dispersal and interchange of individuals between sites, producing a single panmictic population or a meta-population structure, would support a landscape-scale approach. In contrast, if local populations are more strongly differentiated, the need to preserve distinct evolutionarily significant units (ESUs) would dictate a more site-based strategy. Such information will also be vital when planning any future (re-)introductions, especially to sites that are small or distant from existing populations.

Outside the Norfolk Broads, the largest population of *P. m. britannicus* once occurred at Wicken Fen in Cambridgeshire, but this died out in the 1940s (Friday, 1997). Repeated attempts to re-establish a population at Wicken all failed. One attempt in 1975 produced an initial increase in numbers, but a severe summer drought in 1976 caused the population to crash, from which it never recovered, eventually dying out in 1979 (Dempster & Hall, 1980). Considerable subsequent effort by the National Trust, owners of Wicken Fen, to improve the habitat for Milk-parsley resulted in another attempt in 1993-4 by introducing larvae (Barnett & Warren, 1995). Adults were seen until 1997 but not thereafter.

Based on our understanding of the ecologies of the Swallowtail and Milk-parsley, three factors seem to have been responsible for the failure to re-establish a permanent population at Wicken. Firstly, the habitat suffered badly from the difficulty of maintaining the water table, because the level of the surrounding landscape had been lowered by agricultural drainage, isolating the reserve as an elevated area of marsh habitat within a drier landscape (Friday, 1997). This had a negative effect on Wicken's Milk-parsley plants, which are more patchy, smaller (many being only about 50cm tall) and shorter-lived than those on the Broads (Dempster *et al*., 1976). Secondly, inappropriate timing of cutting may have been a contributory factor (Rowell, 1986; Harvey & Meredith, 1981). Finally, it is generally agreed that the area of suitable habitat at Wicken is simply too small (24ha) to sustain a population of *britannicus*, due to the inherent vulnerability of small populations to stochastic events.

Imprecision about the ecological conditions needed for successful management of existing and potential sites for the Swallowtail and its foodplant is likely to constrain the investments needed. More detailed research is needed before further translocations are attempted (Borsje, 2005; Sills, 2010). Furthermore, a clear understanding of the genetic structure of existing Swallowtail populations is needed in order to establish how important gene flow is between separate populations. If gene flow between local populations is indeed necessary, introductions to small or single isolated sites may not be sustainable in the long-term. This makes it particularly challenging to design a new network of sites for Swallowtails in the extensive agricultural landscape of eastern England today.

Risk of extinction from sea-level rise

The Broads is an area of international importance and the ecosystems represented there are of great significance to Britain's biodiversity. They cover just 0.4% of the UK's land area but in 2011 an environmental audit based on 11 million records showed that 26% of all UK Biodiversity Action Plan species are found there (Panter *et al*., 2011). Moreover, fen habitat in the Broads is a hotspot for 1519 Species of Conservation Concern, including the British Swallowtail and Milk-parsley. There are no recent records for 423 (28%) of these, 67 of which are believed to be locally or nationally extinct (Panter *et al*., 2011). Tragically, the Broads have been losing species at a rate of six per decade for at least half a century.

Of the 1519 Species of Conservation Concern, there are 66 Broads Regional Specialties, including Milk-parsley and the Swallowtail, that are completely reliant on freshwater fen habitat for their survival (Panter *et al*., 2011). Moreover, vegetation surveys indicate that only 20% of fen is suitable for Swallowtails, with both reed and Milk-parsley growing together (S24 NVC community). We foresee a number of potential challenges that the British Swallowtail, Milk-parsley and the 64 other Broads Regional Specialties will face within just a few decades, but the most alarming of these is the predicted rise in sea level as a direct result of anthropogenic climate change.

The UK Committee on Climate Change said in its 2018 report on *Managing the Coast in a Changing Climate* that a 1m sea-level rise is likely this century. The Broads are extremely vulnerable because the whole area is low lying and close to a long, relatively poorly protected and vulnerable coastline

(Price, 2013). Indeed, even without further sea-level rise, a combination of high tides and onshore wind can send a pulse of highly saline water up Norfolk's rivers, killing fish and aquatic invertebrates and spilling into fens and broads. Such events have already happened, the most recent in 2014 (BBC, 2014), but higher sea levels increase the likelihood and thus probably their frequency.

It appears that "managed retreat" in Norfolk is a more likely strategy than stronger sea defences and that current Coastal Management Plans are inadequate to meet the challenge of sea-level rise (Committee on Climate Change, 2018). Indeed, even if more sea walls were to be constructed, they may not withstand the power of the rising sea. On 12th February 1938 over 30km^2 of land was swamped when the sea wall in north-east Norfolk was breached between Winterton and Horsey (Sainty *et al.*, 1938). The freshwater ecosystems of Horsey Mere and Hickling Broad, two important Swallowtail breeding sites at the north-eastern extremity of the Broads ecosystem (Figure 2), were destroyed and took four years to recover (Buxton, 1942).

Even when sea walls are resilient, they are not impermeable. There is evidence that sea water is being drawn through the Crag aquifer in the Brograve catchment near Horsey, affecting both Horsey Mere and Hickling Broad (Panter *et al*., 2011, p.51). It needs to be borne in mind that seawater entering the marshes at Horsey is below sea and river level and can only be flushed out by being pumped up into Horsey Mere and travelling 30km downriver to Breydon Water at Great Yarmouth, undoubtedly destroying freshwater fish and other species on its way. This adds to the problem of seawater ingress as a result of rising sea levels at Breydon Water, the south-eastern extremity of the Broads.

An overlay of 50cm sea-level rise (i.e. 50% of the predicted rise) on East Anglia's topography (Figure 2) indicates that all the main Swallowtail and Milk-parsley sites in Norfolk would either be inundated or badly affected by saline infiltration and tidal surges. Any engineering projects, such as enhanced sea and river defences would of course mitigate this risk, but such investments are currently far from certain.

Climate change will bring hotter, drier summers to the eastern region, which already has the lowest annual rainfall in the UK. At the same time, analyses from the Office of National Statistics (2018) predict that the eastern region will see England's second highest human population growth rate (7.3%) after London (8.8%) and that Norfolk's population will grow by 14% between 2014 and 2036. Increased demand for freshwater from rivers and the aquifer will reduce the ability of the river systems to flush out any saline incursions, further compromising freshwater quality upstream.

Risk of extinction from hybridization

Thomas and Lewington (2010) listed three episodes of *P. m. gorganus* immigrations into southern England between the mid nineteenth and the mid twentieth century, each of about ten years. More recently, Blencowe & Hulme (2017) report a similar invasion of *gorganus* into Sussex since 2013, including records of successful overwintering. Most larvae have been found on Wild Carrot, Rue (*Ruta graveolus*) or Fennel (*Foeniculum vulgare*). With further climate warming, it seems only a matter of time before *gorganus* establishes a permanent base in southern England.
There is no published information as to whether the spread of *gorganus* presents a threat to the genetic integrity of the endemic British Swallowtail. Blencowe & Hulme (2017) regard this as unlikely, given the current geographical separation, and Eller (1936: pls 11, 16) illustrated what could be significant differences between the male genitalia of *britannicus* (pl. 11, fig. 6; pl. 16, fig. 83) compared with *P. machaon machaon* (pl. 11, fig. 7; pl. 16, fig. 84) and *P. m. gorganus* (pl. 11, fig. 8, pl. 16, fig. 85). Nevertheless, *gorganus* and *britannicus* reportedly will hybridise by hand-coupling in captivity (A. Brazil pers. obs.) and natural hybridisation across the North American range of *Papilio machaon* (*sensu lato*) is extensive and complex. On this basis it seems probable that this will also prove to be the case in the Palaearctic[1]. Separation by habitat or larval foodplant preferences may

[1] Sturm (2017) included six species in the *Papilio machaon* group: *P. hospiton* Géné, 1839; *P. saharae* Oberthür, 1879; *P. machaon* Linnaeus, 1758; *P. polyxenes* Fabricius, 1775; *P. zelicaon* Lucas, 1852; and *P. indra* Reakirt, 1866. However,

therefore be inadequate to maintain segregation of the subspecies if their ranges do eventually overlap. This underlines the importance of developing genomic markers to monitor potential future introgression of *gorganus* genes into the *britannicus* genome.

Conclusions and recommendations

Given the impending risk of severe salinization, the future of fenland habitat in the Broads, together with the British Swallowtail, Milk-parsley and more than 60 other salt-intolerant fenland-dependent species, is insecure. Unless tidal surges and sea-level rise can be controlled, survival of these species in the long term will require the establishment of new populations away from the threat. As no suitable habitat has yet been identified within dispersal range, this cannot happen through natural colonisation. Instead, (re-)introduction and translocation of the species from the Broads populations into carefully researched and selected sites will become the only viable way to secure the Swallowtail's survival in Britain.

The geographic area within East Anglia south of The Wash known as The Fens (as opposed to The Broads National Park to the east) is somewhat safer from the immediate threat of saltwater

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hybridisation is widespread in this complex, including within the highly polytypic *P. machaon* itself (Clarke & Sheppard, 1955; Cianchi *et al.*, 2003; Dupuis & Sperling, 2015; 2016).

Within *Papilio machaon,* Sturm (2017) lists four subspecies in the western Palaearctic, including *P. m. britannicus*, twelve subspecies in the eastern Palaearctic and Asia, and eight in North America. According to Sturm these last include *P. m. joanae* Heitzman, 1973, and *P. m. brevicauda* Saunders, 1869, but Dupuis & Sperling (2015) are clear that these two taxa both represent separate species that have arisen though hybridisation – taking the total number of species currently recognised within the *machaon* group to eight.

It has been widely assumed that *P. m. britannicus* is taxonomically closest to, but distinct from, the European continental subspecies *P. m. gorganus* Fruhstorfer, 1922 (type locality: Germany, Austria, central Europe). Although the differences in external appearance are subtle, Eller (1936) nevertheless placed *P. m. britannicus* in its own "Rassengruppe", one of 13 'racial groups' into which he divided the 35 subspecies that he recognised. In his 'Determination Table' Eller (1936: 84 *et seq*.) included just two subspecies within the "Gorganus-Gruppe": *P. m. gorganus* and *P. machaon machaon* (type locality: Sweden). Sturm (2017) proposes that *gorganus* should be synonymised under the nominotypical race. For our purposes here, this synonymy is not accepted – but clearly there is a pressing need for a modern account of the infraspecific taxonomy and phylogenetics of *P. machaon* (*sensu lato*) across the Palaearctic, with special reference to Western Europe and North Africa.

incursion. Currently only about 1% of the former fenland area is remnant fen habitat, but emerging partnerships between public, private and voluntary organisations including local authorities, nature conservation bodies, farmers, landowners and academic institutions have developed a vision for the Fens between Cambridgeshire and Lincolnshire which sees sustainable wetlands restored, recreated and re-connected (Fens for the Future, 2012). Such stakeholder partnerships may offer a promising future for fenlands and the Swallowtail. Indeed, a significant amount of fen has already been recreated in the last 40 years, often with considerable public funding (Fens for the Future, 2012). Four current fen restoration schemes in particular present possible sites for Swallowtail introductions.

1. Since 1995 RSPB has created nearly 400 ha of wetland habitat at Lakenheath including reedbed, ungrazed fen and wet grassland. Milk-parsley is absent.
2. The Great Fen project is a 50-year plan to create a 3,700ha wetland, connecting Woodwalton and Holme Fens (both National Nature Reserves) and eventually to network with Wicken Fen, Chippenham Fen and the washlands of the rivers Great Ouse and Nene, many of which are also undergoing restoration and extension projects. Milk-parsley is present at Wicken but not elsewhere in the Great Fen.
3. The Norfolk Wildlife Trust is creating 130 ha of wetland in the Wissey Valley Living Landscape project at Hilgay (Norfolk Wildlife Trust, 2018).
4. A study of Milk-parsley ecology in the 500 ha Shapwick Heath National Nature Reserve in the Avalon Marshes complex of the Somerset Levels has indicated that suitable habitat, safe from the risk of salinization, is present there (Borsje, 2005).

A successful project would require introduction of Milk-parsley in some cases, and careful management of the ecological conditions needed by Milk-parsley populations in all of them. Some sites would certainly be large enough to introduce the butterfly at a number of locations. Such a meta-population introduction structure would mitigate against the risk of extinction faced by isolated reintroductions into small sites, such as occurred at Wicken Fen.

These proposals for East Anglia and Somerset are consistent with the UK government's plan: *A Green Future: Our 25 Year Plan to Improve the Environment* (H.M. Government, 2018) which describes a *Nature Recovery Network* to protect, restore and reintroduce wildlife, and foresees measures to adapt to climate change and reduce the risk from flooding. Meanwhile, the entomological community has a longstanding code of practice for insect re-establishments (Joint Committee for the Conservation of British Insects, 1986) and is well-placed to support such a vision.

These initiatives make sound economic as well as environmental sense. Rare species are part of the nation's natural capital and although a detailed cost-benefit analysis is beyond the scope of this paper, it is notable that natural history enthusiasts travel from across Britain and further afield to see the British Swallowtail. No-one has yet estimated the positive economic impact that translocation of the Swallowtail to additional sites might have, but it may be significant.

Whilst, there is no immediate reason (or indeed means) to protect the British Swallowtail from hybridisation with its continental conspecific, *P. m. gorganus*, the northward spread of the latter subspecies should be carefully monitored. If the two subspecies ever came into contact, conservationists could be faced with the first documented case in Britain of extinction of an insect by hybridisation (Rhymer & Simberloff, 1996; Todesco *et al*. 2016).

Acknowledgements

Our thanks go to the following: two anonymous reviewers; Trustees of the Ted Ellis Trust and the Swallowtail and Birdwing Butterfly Trust for their support; Will Fitch (Reserve Manager) and and Kevin Radley (Volunteer Guide) at the Wheatfen Reserve for personal observations and excellent facilities; the Royal Entomological Society for a generous grant to support the meeting; Paul Hardy for GIS and IT support; Sue Arnold, Mel Collins, Margaret Hardy, and Jane Tebbit for additional assistance. The authors have no conflicts of interest in relation to this review.

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FIGURE CAPTIONS

Figure 1:

Swallowtail records for Norfolk, UK, 2000–2018. Large dots denote multiple sightings and evidence of breeding; medium-sized dots denote several sightings but no breeding; small dots represent single sightings. Rectangle on whole-country map shows position of main map. Grid lines are 10km apart.

Figure 2:

Distribution of the principal British Swallowtail breeding sites (butterfly symbols) in relation to areas projected to be affected by future sea-level rise. Darker shading (superimposed over satellite image) denotes areas projected to be inundated by a 0.5m sea level rise above current Mean Higher High Water mark (MHHW). Black denotes areas of existing open water. Sources: Swallowtail breeding sites, K. Radley; sea-level prediction, Surging Seas Risk Zone Map (https://ss2.climatecentral.org).

Figure 1

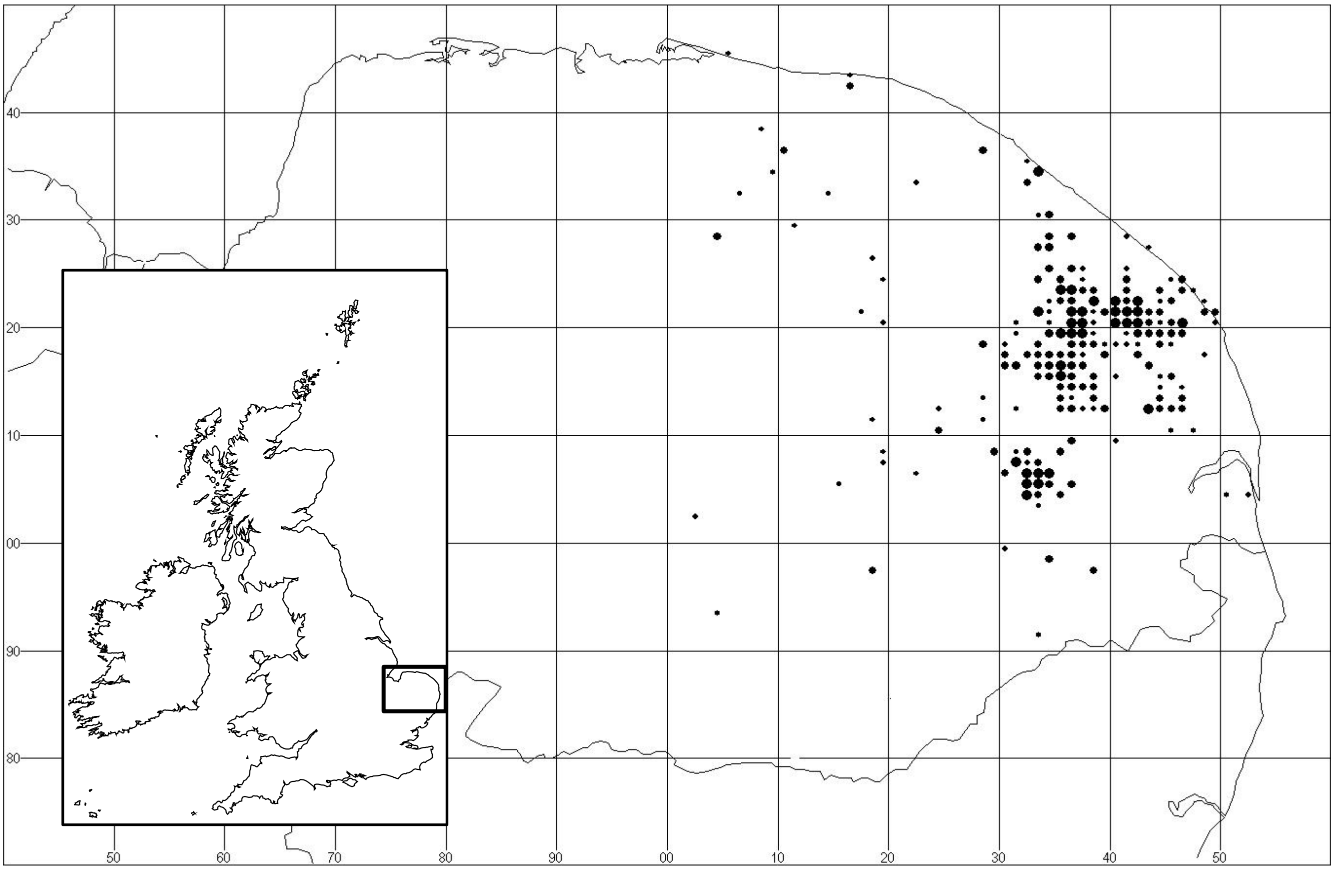
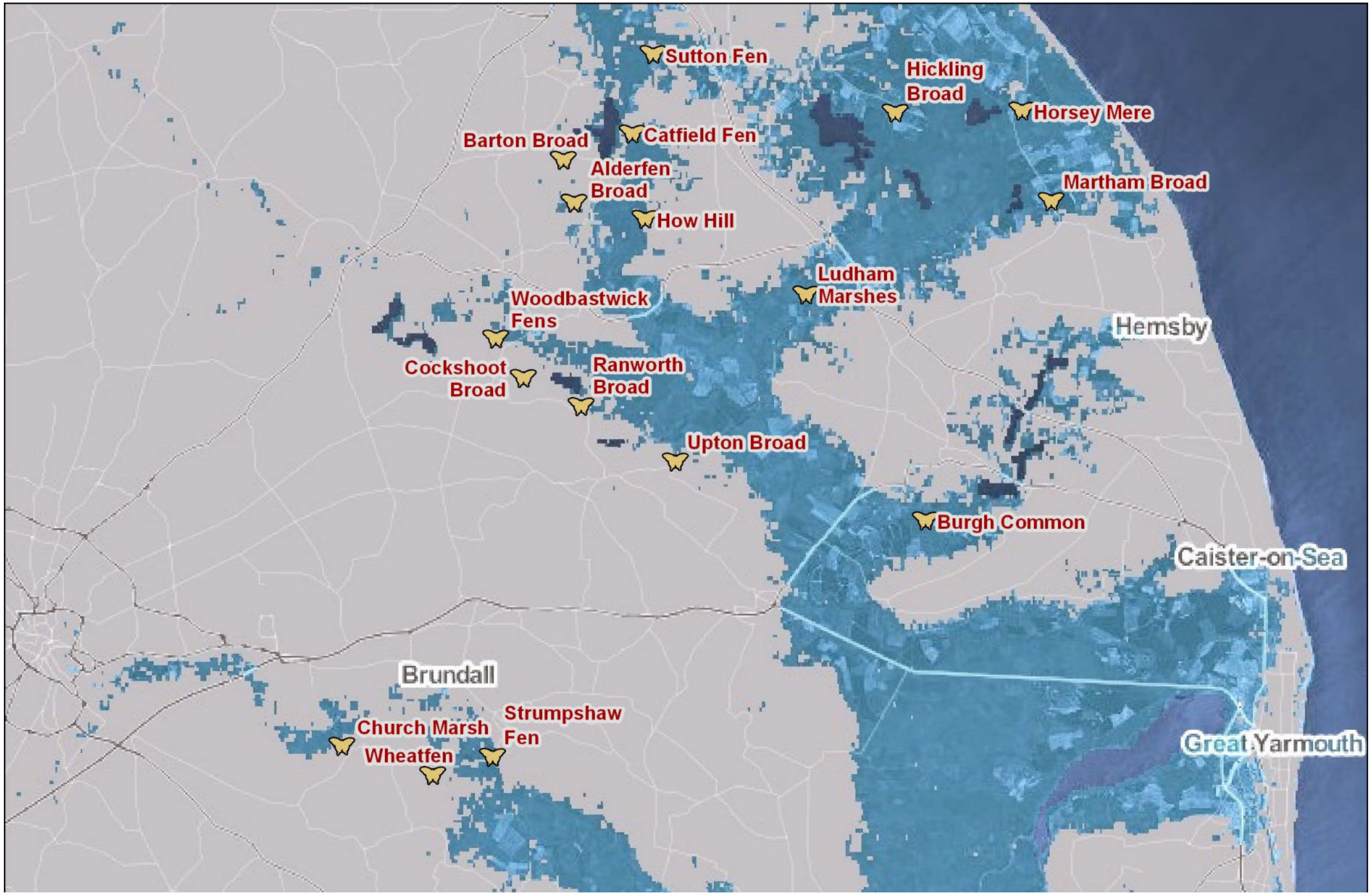


Figure 2


Sutton Fen
Hickling Broad
Horsey Mere
Barton Broad
Catfield Fen
Alderfen Broad
How Hill
Martham Broad
Ludham Marshes
Woodbastwick Fens
Hemsby
Cockshoot Broad
Ranworth Broad
Upton Broad
Burgh Common
Caister-on-Sea
Brundall
Strumpshaw Fen
Church Marsh
Wheatfen
Great Yarmouth