# The History, Ecology, and Reintroduction of the Chequered Skipper Butterfly *Carterocephalus palaemon* in England

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# Declaration

I confirm that this thesis is the result of work done during the period of registration, is my own work (except where clearly indicated in the text), and no part of it has been – or is being – concurrently submitted for another degree or qualification at the University of Northampton or other university or similar institution.

Signed: Jamie Paul Wildman

# Abstract

Over 41% of global insect species have declined over the past decade, compared with 22% of vertebrate species. For Lepidoptera, 53% of species are declining and 34% are threatened globally. Since 1976, 80% of butterflies species have declined in either abundance or occurrence or both in the United Kingdom (UK). A total of 24 of 62 (41%) UK butterfly species assessed as part of a 2022 Red List of British Butterflies published by UK conservation charity Butterfly Conservation are classed as Threatened, with a further five (9%) as Near Threatened. The number of Threatened UK butterflies continues to rise and shows no sign of abating. A total of six butterfly species have been declared extirpated in the UK in recorded history, including the chequered skipper butterfly *Carterocephalus palaemon*, which was lost from England in 1976 after a precipitous decline that was believed to have started in the 1960s. However, due to a paucity of available data, the species' historic distribution and abundance in England was poorly understood.

As part of the Butterfly Conservation-led reintroduction of *C. palaemon* to Rockingham Forest in Northamptonshire known as Back from the Brink – Roots of Rockingham (2018-21), a research project was developed to enhance the 266 historic records of *C. palaemon* that exist on the Butterflies for the New Millennium (BNM) database through museum and other uncollated data, and use the enhanced dataset used to analyse the pattern of *C. palaemon* decline and extirpation in England. In 2018, 42 adult *C. palaemon* were released at Fineshade Wood using stock translocated from donor populations in Belgium. The Fineshade Wood population was sampled in 2019, 2020, and 2021 to estimate its size, determine the mobility and dispersal of individual butterflies, and describe the ecology of the reintroduced species. A complementary review was undertaken to determine the global status of butterfly reintroductions, and the impact of woodland management on other taxa at Fineshade Wood was assessed.

A novel, non-invasive photographic-mark-recapture (PMR) population sampling technique was developed using the unique wing markings of *C. palaemon* to detect the movements and lifespan of individual butterflies photographed during timed counts at Fineshade Wood. Population size was estimated annually by a POPAN model using PMR data and tested against encounter rates generated from *C. palaemon* timed count data to determine the reliability of this sampling method. In addition, over 3500 new historic *C. palaemon* records were collected from museums and other sources of uncollated data and added to the existing BNM dataset. Extinction trajectories were generated to identify a pattern of decline in England that started approximately a decade earlier than the 1960s, in the late 1940s-early 1950s. Spatiotemporal variables tested for association indicated that colonies at larger sites, and larger sites in metapopulation networks (<2km apart) were buffered against extirpation to a greater extent than more isolated colonies at smaller sites.

A global review of butterfly reintroductions found that reintroduction had been attempted in 394 cases in the UK and Ireland, 69 in Europe, 48 in North America, and 15 in the rest of the world (526 total). When considering cases only with definitive outcomes (348 cases), 36.8% reported reintroduction success. The UK and Ireland had the largest number of successful cases (87) and Europe the highest percentage of successful cases (40.7%). Abundance and density of primary *C. palaemon* nectar source bugle *Ajuga reptans* on woodland rides was found be positively correlated with adult female *C. palaemon* encounter rates. Butterfly species richness and abundance was higher on managed versus unmanaged woodland transects. An increase in survey effort through moth trapping associated with Back from the Brink – Roots of Rockingham was considered responsible for increases in moth species richness and abundance.

PMR enabled us to detect that individual adult *C. palaemon* moved up to 1.76km from initial capture point using a ride-level measurement technique, and five of 30 *C. palaemon* photo-recaptured between

2019-21 (16.7%) moved a total distance >1km between captures, belying the sedentary reputation of the species. Gross population size was estimated at 314 in 2019, 332 in 2020, and 721 in 2021. Statistically significant correlation coefficients between daily *C. palaemon* timed count encounter rates and daily population size estimates generated from PMR data were only found when 2019-21 data was combined. Broad agreement between model estimates and *C. palaemon* encounter rates increased confidence in the accuracy of population size estimates that can be generated using less-intensive sampling methods such as timed counts.

The results of this thesis show the importance of provision of suitable habitat within woodland through wide rides, good landscape permeability and site connectivity within landscapes to support reintroduced populations of *C. palaemon* in England. The value of museum and other sources of uncollated data for describing the historic distribution, abundance, and timings of decline of endangered or extinct UK butterfly species is also demonstrated. In conclusion, given habitat is being restored across Rockingham Forest networks to improve suitability for *C. palaemon* and the mobility of photo-recaptured individual butterflies at Fineshade Wood is encouragingly high, there is reason to be optimistic about the future of *C. palaemon* in England.

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## Notes

Several chapters in this thesis are multi-authored, since it is the intention to submit them as manuscripts to journals for publication. This has invariably led to some repetition in the text.

## Recommended citations

### Thesis

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# 1

# General Introduction

## 1.1 Global Biodiversity and Butterfly Decline

In 2019, an Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Global Assessment Report found that up to one million animal and plant species are now threatened with extinction. Average abundance of native species in land-based habitats has fallen by at least 20% since 1900. The average proportion of terrestrial, freshwater, marine vertebrate, invertebrate, and plant groups threatened with extinction stands at 25% (IPBES, 2019). International Union for Conservation of Nature (IUCN) Red Lists point towards decline in abundance and diversity for a significant fraction of a wide range of pollinator groups, such as birds, lizards, bees, hoverflies, and butterflies (Green, 2017; Ollerton, 2021).

There are around 20,000 butterfly species in the world, and one in eight of all described species on the planet is either a butterfly or moth (Chakravarthy and Sridhara, 2016). A recent study by Sánchez-Bayo and Wyckhuys (2019) shows that 53% of global Lepidoptera species are declining and 34% are threatened. In Europe, 37 (9%) of 435 butterfly species assessed for an IUCN Red List are classified as Threatened (Critically Endangered, Endangered, or Vulnerable) and 44 species (10%) as Near Threatened according to quantitative criteria used for the compilation of Red Lists of threatened species globally (Mace and Lande, 1991; IUCN, 2001; Mace *et al*., 2008; van Swaay *et al.*, 2010). However, a comparison of monitoring data for some grassland species shows that coarse-scale grid cell data and actual population trends strongly underestimate extinction risks. The IUCN Red List should therefore be interpreted as a conservative estimate of the threat to European butterfly species (van Swaay *et al*., 2011).

A European Grassland Butterfly Indicator from 16 European countries shows that grassland butterflies have declined by 39% since 1990 (Warren *et al*., 2021). In the Netherlands and Flanders (Belgium), 20% and 29% of butterflies have been declared extinct, respectively (Warren *et al*., 2021). The United Kingdom (UK) has lost a net total of four species (6%) since 1851: the large copper *Lycaena dispar* (c. 1851), mazarine blue *Cyaniris semiargus* (c. 1903), black-veined white *Aporia crataegi* (c. 1925), and large tortoiseshell *Nymphalis polychloros* (c. 1980s). According to the 2022 Red List of British Butterflies published by UK conservation charity Butterfly Conservation, 24 of 62 species assessed (41%) are classed as Threatened (eight Endangered and 16 Vulnerable), with a further five (9%) as Near

Threatened. The number of Threatened butterfly species in the UK continues to rise and shows no sign of abating (Shirt, 1987; Warren *et al*., 1997; Fox *et al*., 2010; 2022).

## 1.2 Butterflies as Biodiversity Indicators

Pollinators such as butterflies are a vital ecological bridge between the flowering plants they pollinate, the food those plants provide for herbivores and frugivores, and predators that prey upon butterflies, such as dragonflies, birds, and spiders (Stork, 2018; Schowalter, 2018; Ollerton, 2021). Butterflies are also an excellent environmental indicator group: they are highly visible and easy to count, broadly representative of a wide range of other invertebrates including moths, react quickly to subtle habitat or climatic change, and their presence and absence cannot be predicted using vegetation-based indicators alone (Erhardt and Thomas, 1991; Dennis *et al.*, 2003; Chakravarthy and Sridhara, 2016; An and Choi, 2021). Consequently, ecologists have widely used butterflies as model organisms to study the effect of habitat loss and fragmentation, and climate change (e.g. Warren, 1992; Hanski and Gilpin, 1997; Thomas, 2005; Maes *et al.*, 2019; Bladon *et al.*, 2020). Solutions to restore biodiversity and butterfly species richness and abundance include comprehensive landscape-scale conservation programmes (e.g. Butterfly Conservation, 2018; European Commission, 2021). These have helped species such as the high brown fritillary *Fabriciana adippe* move from Critically Endangered to Endangered, and the Duke of Burgundy *Hamearis lucina* and pearl-bordered fritillary *Boloria euphrosyne* move from Endangered to Vulnerable in the UK.

An absence of butterflies means an absence of key barometers to judge the health of environments. The reestablishment of threatened or extirpated butterfly species through reintroduction is, therefore, an important part of conservation practice (e.g. Marttila *et al*., 1997; Wynhoff, 2001; Thomas *et al*., 2009; Fred and Brommer, 2015). A reintroduction is defined as an attempt to reestablish a species (a taxonomic unit) in an area which was once part of its indigenous range, but from which it has been extirpated or become extinct (Invertebrate Link, 2010; IUCN/Species Survival Commission [SSC], 2013). Butterfly reintroduction biology is a rapidly developing field which now uses genetic, climatic, microbiological, distributional, and vegetation data to inform release site and donor population selection (e.g. Andersen *et al*., 2014; Kuussaari *et al*., 2015; Dincă *et al*., 2018; Maes *et al*., 2019; Nakahama *et al*., 2022).

## 1.3 Benefits of Butterfly Reintroductions

Reintroductions and conservation translocations reverse biodiversity decline, increase species richness, and improve ecosystem health (e.g. IUCN/SSC, 2013; Brazier *et al.*, 2020; Ratajczak *et al.*, 2022). A butterfly reintroduction results in socioeconomic, ecological, and environmental benefits beyond the addition of a new biodiversity indicator to a landscape. High-profile projects such as butterfly reintroductions are vessels for effectively communicating conservation objectives to the media and general public. They have greater reach and engagement than subtler conservation projects occurring on smaller scales, such as the protection of existing species (see O' Riordan, 2021). Coordinated management can improve habitat quality for a range of native wildlife, such as invertebrates, birds, and reptiles, which can be monitored as target species alongside a reintroduced butterfly to evidence wider ecosystem benefits. A successful reintroduction is, therefore, an important demonstration that conservation lessons can be learnt and loss reversed, counteracting a predominantly pessimistic outlook for invertebrates caused by declining abundance, distribution, and richness trends (e.g. Shirt, 1987; Warren *et al.*, 1997; Fox *et al.*, 2010; 2022; van Swaay *et al.*, 2011; IPBES, 2019; Sánchez-Bayo and Wyckhus, 2019; Warren *et al.*, 2021). Publicity generated by butterfly reintroduction can also increase wildlife tourism to an area, as well as encourage participation in volunteer monitoring programmes, guided walks, and other family engagement events.

## 1.4 Extirpation of the Chequered Skipper *Carterocephalus palaemon* in England

The chequered skipper butterfly *Carterocephalus palaemon* (Pallas, 1771) was declared extirpated in England in 1976 and recommended for reintroduction in 1986 (Collier, 1986; Warren, 1990) (Figure 1.1). In response, the Nature Conservancy Council (NCC) – a UK government agency responsible for managing National Nature Reserves (NNRs) and other conservation areas between 1973-91, which is now known as Natural England – funded a three-year study into the butterfly's ecological requirements in Scotland (Ravenscroft, 1992). The British Butterfly Conservation Society (now Butterfly Conservation) formed a Chequered Skipper Working Party to investigate the possibility of reestablishing the species in England as part of a wider conservation strategy (Steel, 1990). Martin Warren produced a report on the ecology and habitat requirements of *C. palaemon* in northern Europe as part of this initiative (Warren, 1990), and later studied the butterfly in northern France and southern Belgium, accompanied by Neil Ravenscroft (Ravenscroft and Warren, 1992; Ravenscroft, 1994a; 1994b).

**Figure 1.1**: ♂ (male) *C. palaemon* at Fineshade Wood, showing underside (left) and upperside (right) of forewings and hindwings (Image credit: Andy Wyldes and David James).

Chambers Farm Wood in the Bardney Limewoods complex in North Lincolnshire was selected for an experimental reintroduction in the 1990s (Warren, 1995a; Ravenscroft and Warren, 1996). Between 1995-99, *C. palaemon* eggs and adults were collected from Spincourt, Rafour, Villecloye, Chantemelle, and Fôret de Lachalade and Haute Chevauchee areas of the Fôret d'Argonne in France, which was adopted as the main donor population for the reintroduction (Warren, 1995b; Moore, 2004). Captive breeding was attempted, however stock quality of both translocated adult and captively reared eggs was suspect: many adults were released in unmated or poor condition, and eggs had been subjected to laboratory-based hostplant and humidity experiments to synchronise emergence with wild *C. palaemon*. Weather conditions were poor in both main release years and high-quality habitat was limited (J. Moore, personal communication). The reintroduction was ultimately unsuccessful.

## 1.5 Reintroduction of *C. palaemon* to England

A second project to reestablish *C. palaemon* in England was developed in the 2010s by Butterfly Conservation. The Rockingham Forest landscape of Northamptonshire and Cambridgeshire was chosen as a reintroduction site given it was the last stronghold of the species in England (Ravenscroft 1994b; Asher *et al*., 2001; Wildman *et al*., 2022). A landscape is here defined as a mosaic of heterogeneous land forms, vegetation types, and land uses (Urban *et al*., 1987), and a sub-landscape as an aggregation of geographically distinct, spatially interrelated features of interest within a wider landscape.

Donor populations were selected using a combination of distribution data and environmental variables (Corine Land Cover and climate data) from four regions in Belgium, two in the Netherlands, and one in Argyll, Scotland. Models were calibrated with these regions and projected onto the Rockingham Forest landscape. The Fagne-Famenne-Calestienne region of Belgium was chosen based on model outputs and additional expert knowledge of hostplant abundance and population size (Bourn, 2019; Maes *et al*., 2019) (Figure 1.2).

**Figure 1.2**: A typical herb-rich woodland ride in Belgium, from which adult *C. palaemon* were collected in 2018. The surrounding high forest only shades half of the ride due to its width. A small stream bordered by light scrub runs along its centre.

A founder population of 42 adults (32 females and 10 males) was translocated from Belgium and released at Fineshade Wood in 2018. A second release of 24 adults (12 females and 12 males) took place in 2019. The initial reintroduction phase formed part of a project colloquially known as Back from the Brink – Roots of Rockingham (2018-21). Back from the Brink was a nationwide initiative and consisted of 19 projects funded by a £4.6m grant from the Heritage Lottery Fund, the People's Postcode Lottery, the Garfield Weston Foundation, the Esmée Fairburn Foundation, and Forestry Commission England, as well as local delivery partners. Roots of Rockingham cost £350,540, and covered an extensive programme of volunteer training, education, and public activities over four years, including approximately £10,000 per year translocating and releasing *C. palaemon* in England (see O'Riordan, 2021). A complementary programme of Rockingham Forest management works was developed in partnership with Natural England and Rethink Nature. Over 7km of woodland rides were widened and

32ha of vegetation managed to improve habitat quality for *C. palaemon* and 14 other priority species, including dingy skipper *Erynnis tages* and grizzled skipper *Pyrgus malvae*. The reintroduction continues through a second phase funded by the Green Recovery Challenge Fund (2021-23). A further release of 50 adult *C. palaemon* occurred in 2022. The population has been annually monitored since 2018 using a combination of paid staff, timed count volunteers, and research students.

## 1.6 Taxonomy

*C. palaemon* is first described as *Papilio palaemon* (Pallas, 1771) – a synonym of *C. palaemon.* It is also described as *P. brontes* (Denis and Schiffermüller, 1775) and *P. paniscus* (Fabricius, 1775). Several North American subspecies have also been described – the first of these being *C. p. mandan* (Edwards, 1863). Lederer (1853) cites three nominal species of the family Hesperiidae (Latreille, 1809) as belonging to the Holarctic genus *Carterocephalus* – the first of these being *P. paniscus.* Evans' (1955) *Carterocephalus* genus is characterised by its porrect, hairy palpi (with a slender third segment), a stout antennal club, long discal cell on the hindwing compared to other groups of skippers, and by its lack of secondary sexual characters. Speyer (1897) diagnoses the group similarly. Aurivillius (1925) describes the subfamily of Heteropterinae 'skipperlings', which includes 14 genera alongside *Carterocephalus*. There are 16 *Carterocephalus* species globally – a majority of which are endemic to China. Taxonomic order and colloquial names of UK and European butterfly species mentioned in this thesis follow Tolman and Lewington (2008) and Thomas and Lewington (2016).

## 1.7 Distribution

*C. palaemon* is found from the north Pyrenees through central France and north Italy (where it is common in the Dolomites) to the Arctic circle, the Balkans, and Northern Greece. Outside of Europe, the butterfly is found in Central and North Asia to Japan, and North America. *C. palaemon* is absent from the Iberian Peninsula except the Val d'Aran (east Pyrenees), west and south France, the Italic Peninsula, north Belgium, north Holland, Denmark, south Sweden, Albania, the Republic of Macedonia, and southeast Bulgaria (Tolman and Lewington, 2008). A geographically distinct population located in western Scotland was first documented in the 1940s (Mackworth-Praed, 1942), although the first sighting may have been decades earlier (Joicey and Noakes, 1907; Thomson, 1980). *C. palaemon* is considered nationally scarce in the UK but not currently regarded as threatened in Europe. It is categorised as Least Concern on both IUCN Europe and EU27 Red Lists (van Swaay *et al.*, 2010; Fox *et al.*, 2022). *C. palaemon* was first recorded in England in 1798 and last recorded in 1976 (Archer-Lock, 1982; M. Fuller, personal communication). Genetic studies have found no difference between the extirpated English butterfly and those found in Scotland (Joyce and Pullin, 2004).

## 1.8 General Ecology

*C. palaemon* is a univoltine species that flies between May-June at lower altitudes, and July in mountainous areas of southern Europe above 1600m (Higgins and Riley, 1983; Tolman and Lewington, 2008; Haahtela *et al.*, 2011). It exhibits a mixture of gold, light browns, and creams on a dark brown ground colour in a chequered pattern that gives the butterfly its name, although it is colloquially known as the arctic skipper in North America (Bink, 1992; Bird *et al.*, 1995; Eeles, 2019). The butterfly's small size (male wingspan is approximately 29mm with the female slightly larger at 31mm) and fast, skipping flight over grass-tops complicates detection and tracking. When at rest with wings closed on the inflorescence of grasses such as wood small-reed *Calamagrostis epigejos*, meadow foxtail *Alopecurus pratensis*, and sweet vernal-grass *Anthoxanthum orodatum*, the butterfly is especially well-camouflaged, but can be easily disturbed in warm and sunny weather (typically >16ºC), leading to rapid, evasive flights.

Male *C. palaemon* are territorial, and adopt perches on grass inflorescence in anticipation of mating opportunities with the more transient female butterfly. Males take flight to intercept and chase off encroaching invertebrates before circling back to the same perch or one nearby offering similarly good visibility of surrounding vegetation (Ravenscroft, 1992; Moore, 2004). This behaviour is interspersed with short spells of nectaring, typically on flowers of low-growing bugle *Ajuga reptans*. In contrast, female *C. palaemon* engage in prolonged bouts of nectaring, often in carpets of *A. reptans* that permit shorter flights between spikes. *C. palaemon* is known to nectar on 18 species of flowering plant but expresses a strong preference for blue, pink, and purple flowers such as *A. reptans,* bush vetch *Vicia sepium*, bluebell *Hyacinthoides non-scripta*, *a*nd marsh thistle *Cirsium palustre.* Other nectar sources include pignut *Conopodium majus*, heath spotted-orchid *Dactylorhiza maculata*, bell heather *Erica cinerea*, cross-leaved heath *Erica tetralix*, wild strawberry *Fragaria vesca*, ground ivy *Glechoma hederacea*, bramble *Rubus fruticosus* agg., and germander speedwell *Veronica chamaedrys* (Frohawk, 1934; Farrell, 1973; Collier, 1978, 1986).

Females are more elusive still than males, preferring to flutter amongst denser, scrubbier vegetation in search of suitable hostplants on which to lay eggs. Females lay singularly on the underside of grass blades of *C. epigejos* (Warren, 1990), *A. pratensis* (Tolman and Lewington, 2008), purple moor-grass *Molinia caerulea* (Weidemann, 1988), false brome *Brachypodium sylvaticum* (e.g. Rollason, 1908; Wood, 1908; Ravenscroft, 1991; Ravenscroft and Warren, 1992), heath false brome *B. pinnatum* (Collier, 1966), hairy brome *Bromus ramosus* (Frohawk, 1892), and Yorkshire fog *Holcus lanatus*

(Moore, 2004). In former English populations, both *Brachypodium* spp. were believed to be the main hostplants (Emmet and Heath, 1989). Fletcher (1899) found that larvae "fed freely on all grasses offered to them, but seemed to prefer wide-leaved species." Collier (1986) noted the importance of a combination of primary and secondary hostplants in sunny, sheltered positions at Castor Hanglands – a former stronghold of the species in Cambridgeshire. Males have been known to live for up to 18 days at Ariundle in Scotland, and females thought to fly >1km in round trips from pupal eclosion sites to nectaring, mating, and egg-laying grounds (Ravenscroft, 1992). Variation consists mainly of enlargement of gold and cream markings, which may form a confluent band on the upperside forewings (upf) (aberration (ab.) *scabellata*), or reduction to a single central marking on the upperside hindwing (uph) (ab. *extrema* Dioszeghy). An albino form with dark markings replaced by a pale brownish grey is known as ab. *albinotica* Goodson (Russworm, 1978).

## 1.9 Research Aims

In conjunction with the reintroduction of *C. palaemon* to England, this research project was developed with several key aims, which are addressed through the following five chapters and a General Discussion. In Chapter Two, we will review the global status of butterfly reintroductions and determine the success rate of cases in the UK and Ireland, North America, and the rest of the world. In Chapter Three, we will use historic data from museums, private collections, published and unpublished texts, and an existing Butterflies for the New Millennium (BNM) database to determine the former distribution and range of *C. palaemon* in England. In Chapter Four, we will use the historic data from Chapter Three to analyse the species' pattern of extirpation and relate it to anthropogenic and environmental drivers of decline. Following this, in Chapter Five, we will use 2019-21 data from the reintroduced population at Fineshade Wood to study the mobility, dispersal, and lifespan of individual adult butterflies at the release site. In Chapter Six, we will analyse behaviour such as roosting and microhabitat selection, describe the butterfly's relationship with primary nectar source bugle *Ajuga reptans*, and explore how *C. palaemon* may utilise ride features for navigation and foraging purposes. Lastly, in the General Discussion, we will provide an overview of the reintroduction project to 2021 and recommend best practice for future butterfly translocations. The benefits of management work to other taxa will also be summarised here, followed by a more detailed analysis in Appendix Four.

# 2

# A Global Review of Butterfly Reintroductions

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## Abstract

Butterfly biodiversity is declining worldwide at an alarming rate, and reintroductions are increasingly being seen as an important part of conservation practice to reverse regional extinctions and increase distribution and abundance of rare, endangered, or at-risk butterfly species. However, cases are poorly documented and previous reintroduction reviews have only covered specific geographic areas rather than assessing the status of butterfly reintroductions worldwide. Here, we add reintroduction case data published in a 1990 Joint Committee for the Conservation of British Insects (JCCBI) review of butterfly reintroductions (Oates and Warren, 1990) and data collated for an unpublished 2019 Butterfly Conservation review of cases in the UK and Ireland to a desk-based study of worldwide reintroductions to create a single dataset of cases. We find that introduction, reintroduction, and colony reinforcement has been attempted in 443 cases in the UK and Ireland, 69 in Europe, 50 in North America, and 15 in the rest of the world (577 cases in total) for 67 butterfly species. We conclude that: I) peer-reviewed research, empirical data, and clear methodology is often unavailable for individual reintroduction projects, II) systematic documentation of cases and peer-reviewed publication of outcomes is essential to further butterfly reintroduction biology, and III) a major research project to determine the true extent of sanctioned and clandestine reintroductions worldwide is necessary in order to communicate lessons learnt and best practice to a wider international scientific audience.

## 2.1 Introduction

Butterfly species are experiencing a long-term decline in distribution and abundance. Butterfly distributions decreased by 80% between 1890-1940 and overall numbers have fallen by 50% since 1990 in the Netherlands. In the UK, overall numbers have declined by around 50% since 1976. Extirpation of 8% of resident species has occurred in the UK, 20% in the Netherlands, and 29% in Belgium (Warren *et al*., 2020). In mainland Europe, 37 of 435 assessed species (9%) are classified as Threatened (Critically Endangered, Endangered, or Vulnerable), and 44 species (10%) as Near Threatened – most of which are in urgent need of conservation action according to the IUCN Red List (van Swaay *et al*., 2010). In the UK, 18% (11 species) were considered Near Threatened, Vulnerable, or worse in 1987, which rose to 31% (19 species) in 1997, and 52% (33 species) in 2021 (Shirt, 1987; Warren *et al*., 1997; Fox *et al*., 2022).

The most recent Red List of British butterflies has moved seven species to a higher threat category since 2010 – from Near Threatened to Vulnerable status (Fox *et al*., 2022). In North America, the migratory monarch butterfly *Danaus plexippus* has recently been declared Endangered by the IUCN, threatened by habitat destruction and climate change (Walker *et al*., 2022). In the western United States (US), numbers of individual butterflies have fallen by 1.6% annually since 1977 (Forister *et al*., 2021) – broadly consistent with the rate of decline for invertebrates globally in the Anthropocene (Dirzo *et al*., 2014; Hallman *et* al., 2013; Vogel, 2017; Wagner *et al.*, 2021). Drivers of decline for butterfly species include land use changes through urbanisation and agricultural intensification, habitat quality decline due to changing forestry practices, inappropriate site management and abandonment, climate change, and insecticide use, amongst others (e.g. Collier, 1986; van Swaay and Warren, 1999; Schweiger *et al.*, 2008; Settele *et al*., 2008; Gilburn *et al.*, 2015; Warren *et al.,* 2021).

In order to combat the rapid decline in distribution and abundance of butterfly species, reintroductions have become an important part of modern conservation practice (e.g. Marttila *et al*., 1997; Wynhoff, 2001; Thomas *et al*., 2009; Fred and Brommer, 2015). The UK government has recently released a code and guidance for reintroductions in response to the increased awareness and significance of translocations to restore biodiversity (Department for Environment, Food, and Rural Affairs [DEFRA], 2021a). A reintroduction is defined as "the intentional movement and release of an organism inside its indigenous range from which it has disappeared" (IUCN, 2013). To achieve this for butterfly species, stock must be translocated from a donor population – the "human-mediated movement of living organisms from one area, with release in another" (IUCN, 2013) – to a reintroduction site. This can be either within or outside a species' indigenous range, known or inferred by historical records or physical evidence. In absence of direct evidence to confirm previous occupancy, the IUCN (2013) state that the "existence of suitable habitat within ecologically appropriate proximity to proven range may be taken as adequate evidence of proven occupation." We add that butterfly reintroduction aims to reestablish a viable population lost through extirpation in order to benefit not only the species translocated, but also wider biodiversity and the ecosystem which it occupies. At a site where a butterfly species is extant but in decline, stock can be released to reinforce colonies (Invertebrate Link, 2010). Reintroduction does not have to be direct: a founder population can be introduced by translocating stock from a donor site to a release site, or by translocating to an intermediary for captive rearing prior to reintroduction. Different life-cycle stages and generations can be used, depending on species requirements and project circumstances.

In this chapter, we combine existing UK and Ireland butterfly reintroduction data, published in a 1990 Joint Committee for the Conservation of British Insects (JCCBI) (now Invertebrate Link) report (Oates and Warren, 1990), with data collected for an unpublished 2019 review of reintroductions in the UK and Ireland by Dr Kate Dent on behalf of Butterfly Conservation. These data will be added to new data collected through a desk-based review of global and post-2018 UK and Ireland reintroductions by the lead author to create a single dataset of cases for analysis. We aim to determine the global status of butterfly reintroductions and identify the achievements and shortcomings of butterfly reintroduction biology in 2022. Based on our findings, we offer recommendations on best practice to increase the likelihood of projects reporting successful reestablishments in the future.

## 2.2 Methods

A contract report for the JCCBI, *A Review of Butterfly Introductions in Britain and Ireland* (Oates and Warren, 1990), was used as a source for 323 cases in the UK and Ireland. Data from p.13 of the report were transcribed to a worksheet and consolidated with 114 UK and Ireland cases collated by Dr Kate Dent on behalf of Butterfly Conservation. Global and post-2018 UK and Ireland cases not represented in either the JCCBI report or Butterfly Conservation dataset (140 total) were collated using the following desk-based methods. An online search of peer-reviewed journal articles, published governmental and non-governmental reports, news articles, presentation slides, project web pages, and blog entries was performed to obtain information on reintroduction projects that were in progress or had already been completed. Standard terms such as ‘butterfly translocation’ and ‘butterfly reintroduction’ were used in Google and Bing searches. The University of Northampton’s Northampton Electronic Library Search Online (NELSON) service was used to locate published papers and other printed materials. NELSON returned 134 results for ‘butterfly translocation' and 119 for ‘butterfly reintroduction’, but only five for ‘butterfly reestablishment’. In-text citations were noted during readthroughs of peer-reviewed articles, and reference lists used to identity additional articles. Studies were daisy-chained this way through a search strategy analogous to snowballing (Wohlin, 2014; 2022). A similar approach was used where no citations were present using information extracted from online news articles, blogs, and summary documents. References to species, locations, and years (where available) were entered into search engines and NELSON alongside the aforementioned search terms in order to locate relevant texts. Both colloquial and binomial names of species were used.Data on species reintroduced, total number of cases (site or sites the species was reintroduced to), and reintroduction country (not donor population country of origin) were entered into three columns on a worksheet. A 'case' was defined as a geographically distinct site that butterflies were reintroduced to (which encompassed colony reinforcement), and a 'project' as the overarching reintroduction programme that featured all cases combined. Cases were classified as successful (the text explicitly indicated as such or populations had persisted for more than five years), a failure (clear the reintroduction was not successful), uncertain (due to lack of evidence), too soon to be determined (the project was still in progress or had recently been completed), or initially successful then a failure (if initial signs were promising but reestablishment did not occur). A five-year threshold for project success was used to replicate Butterfly Conservation Red List assessment criteria for establishment as a resident breeding species (Fox *et al*., 2022) for new global and UK and Ireland cases, however the three-year threshold for successful establishment in Oates and Warren (1990) was retained for cases featured in the JCCBI report due to subtle differences in definition (see 2.4, p.11). If the outcome of a new case was not obvious, it was marked as uncertain.

After the worksheet containing raw data was completed, a new worksheet was created to merge 'total number of releases recorded' (Oates and Warren) with 'total number of cases' (Butterfly Conservation), and 'number of establishments reported 1985-88 and outcome awaited' and 'number of establishments poorly documented' (Oates and Warren) with 'uncertain' (Butterfly Conservation). Duplicate cases were then removed. Oates and Warren (1990) made no determination as to the apparent success or failure of reintroductions which they considered to be poorly documented, and did not repeat data categorised in this way in any other columns. 'Successful establishments – colonies now extinct' (Oates and Warren) data were merged with Butterfly Conservation 'failure (long-term)' data. A new column titled 'unsuccessful (short-term)' was created, to which 'initial success, but then failure' (Butterfly Conservation) and 'number of unsuccessful establishments (i.e. populations survived less than 3 years)' (Oates and Warren) data were added. Due to the limited scope of this review, the fate of cases with colonies originally stated as 'still surviving' in Oates and Warren were not independently verified.

New UK and Ireland and global data collated by the lead author were added to the worksheet. Cases were separated by region (UK and Ireland, North America, mainland Europe, and the rest of the world). On another worksheet, cases belonging to different reintroduction projects but the same species were combined to generate a total number of cases per species. Locations were entered into new columns in instances where the same species was reintroduced to multiple countries. Finally, the year of project initiation (i.e. the start date of each reintroduction, not its planning phase) was added to a new worksheet to create a histogram of global cases after 1980 using Microsoft Excel (Microsoft Corporation, 2021).

## 2.3 Results

### 2.3.1 Total Cases and Butterfly Species Reintroduced

We found 443 cases in the UK and Ireland, 69 in mainland Europe, 50 in North America, and 15 in the rest of the world (577 cases in total) for 67 butterfly species. Of these 577 cases, 526 were reintroductions, 27 were instances of colony reinforcement, and 24 where non-native or exotic species had been introduced to UK and Ireland sites outside their indigenous ranges (Table 2.1 – see also Appendix Four, Table A1.1 for full list of species). The marsh fritillary *Euphydryas aurinia* was the most reintroduced butterfly with 82 documented cases in the UK and Ireland and Germany – 24 (29.3%) of which were successful. A total of 23 *E. aurinia* cases were unsuccessful in the short-term, with a further nine considered to have failed in the long-term. The status of 15 cases was uncertain, and it was too soon to judge the outcome of a further five. The Apollo *Parnassius apollo* was the second-most reintroduced butterfly with 50 documented cases globally. However, 23 cases (46.0%) were long-term failures, and only seven (14.0%) resulted in reestablishment. It was too soon to judge the outcome of another 15 *P. apollo* cases (30.0%). The heath fritillary *Melitaea athalia* was the third-most reintroduced butterfly globally with 28 cases – six of which (21.4%) resulted in successful reestablishment.

**Table 2.1**: The number of butterfly species reintroduced globally, total number of cases for each species, and the status of each case (*=non-native species in host country).

| Species | Total number of cases | Total cases reinforcing existing colonies | Success | Failure (long-term) | Uncertain | Too soon to judge | Unsuccessful (Short-term failure) |
|---|---|---|---|---|---|---|---|
| Adonis blue | 18 | 2 | 4 | 3 | 7 | 0 | 2 |
| Apollo | 50 | 0 | 7 | 24 | 0 | 14 | 6 |
| baton blue | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| bay checkerspot | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| black hairstreak | 9 | 0 | 3 | 0 | 4 | 0 | 2 |
| black-veined white | 7 | 0 | 0 | 0 | 2 | 0 | 5 |
| brimstone | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| brown argus | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| brown hairstreak | 3 | 0 | 1 | 0 | 1 | 0 | 1 |
| Camberwell beauty* | 12 | 0 | 0 | 0 | 0 | 0 | 12 |
| chalkhill blue | 9 | 2 | 2 | 0 | 3 | 0 | 2 |
| chequered skipper | 3 | 0 | 0 | 1 | 0 | 2 | 0 |
| Chinese peacock* | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| Cleopatra* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| clouded Apollo | 2 | 0 | 1 | 1 | 0 | 0 | 0 |
| comma | 3 | 1 | 0 | 0 | 2 | 0 | 0 |
| dark green fritillary | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| dingy skipper | 3 | 0 | 1 | 1 | 0 | 0 | 1 |
| Duke of Burgundy | 16 | 1 | 2 | 2 | 7 | 1 | 3 |
| Esper’s marbled white | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| false ringlet | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| gatekeeper | 2 | 0 | 1 | 0 | 1 | 0 | 0 |
| Glanville fritillary | 23 | 1 | 4 | 4 | 8 | 0 | 6 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| grayling | 4 | 0 | 0 | 0 | 2 | 0 | 2 |
| green hairstreak | 2 | 0 | 0 | 1 | 1 | 0 | 0 |
| grizzled skipper | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| heath fritillary | 28 | 0 | 6 | 3 | 7 | 1 | 11 |
| high brown fritillary | 3 | 1 | 0 | 1 | 1 | 0 | 0 |
| Karner blue | 5 | 0 | 4 | 0 | 0 | 0 | 1 |
| Lange's metalmark | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| large blue | 21 | 0 | 10 | 5 | 0 | 1 | 5 |
| large copper | 14 | 0 | 1 | 4 | 4 | 0 | 5 |
| large heath | 3 | 0 | 0 | 0 | 1 | 2 | 0 |
| large tortoiseshell | 10 | 0 | 0 | 0 | 7 | 0 | 3 |
| Lulworth skipper | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| map* | 7 | 0 | 0 | 1 | 0 | 0 | 6 |
| marbled white | 11 | 0 | 4 | 0 | 6 | 0 | 1 |
| marsh fritillary | 82 | 6 | 24 | 9 | 15 | 5 | 23 |
| Miami blue | 4 | 0 | 0 | 3 | 0 | 0 | 1 |
| mottled duskywing | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| northern brown argus | 2 | 0 | 0 | 2 | 0 | 0 | 0 |
| Oregon silverspot | 3 | 1 | 0 | 0 | 0 | 2 | 0 |
| pearl-bordered fritillary | 16 | 0 | 1 | 8 | 4 | 2 | 1 |
| purple copper | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| purple emperor | 16 | 7 | 5 | 0 | 3 | 0 | 1 |
| Quino checkerspot | 7 | 0 | 6 | 0 | 1 | 0 | 0 |
| red-dotted Apollo | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| regal fritillary | 7 | 0 | 3 | 2 | 0 | 2 | 0 |
| Richmond birdwing | 11 | 0 | 2 | 0 | 9 | 0 | 0 |
| ringlet | 4 | 2 | 1 | 0 | 1 | 0 | 0 |
| scarce large blue | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| scarce swallowtail* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Schaus’ swallowtail | 13 | 0 | 0 | 13 | 0 | 0 | 0 |
| Scotch argus | 11 | 0 | 2 | 2 | 1 | 1 | 5 |
| silver-spotted skipper | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| silver-studded blue | 26 | 0 | 14 | 3 | 4 | 1 | 4 |
| silver-washed fritillary | 14 | 1 | 2 | 1 | 2 | 0 | 8 |
| small blue | 17 | 1 | 4 | 1 | 1 | 2 | 8 |
| small pearl-bordered fritillary | 8 | 0 | 2 | 3 | 1 | 2 | 0 |
| small skipper | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| speckled wood | 5 | 0 | 1 | 2 | 2 | 0 | 0 |
| swallowtail | 12 | 0 | 0 | 1 | 9 | 0 | 2 |
| Taylor’s checkerspot | 6 | 0 | 2 | 0 | 0 | 4 | 0 |
| violet fritillary* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| white admiral | 4 | 0 | 0 | 0 | 2 | 0 | 2 |
| wood white | 14 | 0 | 4 | 3 | 1 | 3 | 3 |
| yellowish sedge-skipper | 2 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Total* | *577* | *27* | *128* | *106* | *131* | *50* | *138* |

Reintroduction was attempted once for a total of 16 species (three of which were exotic or non-native species reintroduced to sites outside their indigenous range). All 24 cases of non-native or exotic species introductions resulted in failure or were too poorly documented for their outcome to be determined (Oates and Warren, 1990). However, for non-native and exotic species cases with uncertain outcomes in the UK and Ireland, no native colonies of Camberwell beauty *Nymphalis antiopa* (an occasional migrant to England, with serious reintroduction attempts made the 1950-60s), map *Araschnia levana* (reintroduced in 1914 to the Forest of Dean in Monmouthshire and Symond's Yat in Herefordshire, England), scarce swallowtail *Iphiclides podalirius* (the first attempt in 1861 at Sevenoaks, Kent), or violet fritillary *Boloria dia* (reintroduced to the New Forest in the 1880s and near Dorking, Surrey in

1985) were known to have established breeding colonies (Newman, 1967; Oates and Warren, 1990). All were therefore interpreted as failures.

## 2.3.2 Success Rate of Reintroductions

Of 526 total cases of reintroduction, 128 (24.3%) – less than one in four – resulted in successful reestablishment of butterfly species. The fate of 50 cases (9.5%) was too soon to judge, as some projects were still ongoing or had only recently concluded. For reintroductions that failed, 138 (26.2%) were unsuccessful in the short-term, and 103 (19.6%) were unsuccessful in the long-term (breeding populations were established, but later failed). Numbers of global reintroductions unsuccessful in the long-term were outnumbered by cases with uncertain outcomes (131; 24.9%). Uncertainty was often caused by a paucity of data, lack of clarity in case descriptions, or the limited scope of this review, which did not incorporate direct contact with organisers or stakeholders to ascertain the status of colonies. When considering cases only with definitive outcomes globally, 128 of 348 (36.8%) reported reintroduction success.

In the UK and Ireland, when considering cases only with definitive outcomes, 87 (34.1%) of reintroductions were successful and 168 (65.9%) were failures (Table 2.2). In North America, 15 cases (43.0%) were successful and 20 (57.0%) were failures. In mainland Europe, the number of unsuccessful cases (32; 46.4%) also outnumbered the number of successful cases (22; 31.9%). No reintroductions were found to have failed in the rest of the world, however a paucity of available data was considered responsible for the result. A total of four cases of 15 from the rest of world resulted in successful reestablishment: two cases of Richmond birdwing *Ornithoptera richmondia* in Australia, and one for red-dotted Apollo *P. bremeri* (South Korea) and purple copper *Paralucia spinifera* (Australia), respectively (Mjadwesch, 2008; Sands and New, 2013; Lee *et al.*, 2021).

**Table 2.2**: The total number of cases of butterfly reintroductions, introductions, and reinforcements of extant populations globally, broken down by region.

| Region | Total number of cases | Total cases reinforcing existing colonies | Success | Failure (long-term) | Uncertain | Too soon to judge | Unsuccessful (Short-term failure) |
|---|---|---|---|---|---|---|---|
| UK and Ireland | 443 | 25 | 87 | 62 | 117 | 24 | 130 |
| North America | 50 | 2 | 15 | 18 | 4 | 9 | 2 |
| Mainland Europe | 69 | 0 | 22 | 26 | 1 | 15 | 6 |
| Rest of the world | 15 | 0 | 4 | 0 | 9 | 2 | 0 |
| *Total* | *577* | *27* | *128* | *106* | *131* | *50* | *138* |

## 2.3.3 Life-Cycle Stage at Reintroduction

Most projects chose to reintroduce either adults or larvae to sites, and quantities released per project varied widely (Table 2.3). Captive rearing and release of large quantities of larvae was a feature of some *Euphydryas* spp. reintroductions in North America and the UK and Ireland, such as Quino checkerspot *E. editha quino* (Longcore and Bonebrake, 2012; Strahm, 2018; Williams-Anderson, 2019), Taylor's checkerspot *E. e. taylori* (Potter, 2016), bay checkerspot *E. e. bayensis* (US Bureau of Reclamation, 2018; Curry, 2019), regal fritillary *Speyeria idalia* (Becker, 2016), and *E. aurinia* (Porter and Ellis, 2010; Davis *et al.*, 2021). Approximately 10,000 *E. e. bayensis* larvae were released in 2013 at Tulare Hill and Edgewood Nature Reserve in California by the Creekside Centre for Earth Observation, and 42,000 *E. aurinia* larvae as part of a Butterfly Conservation-led landscape-scale reintroduction to Cumbria, England, in 2007. The reintroduction of the Miami blue *Cyclargus thomasi bethunebakeri* to the Florida Keys saw 276 adults and 3,277 larvae released between 2007-08 as part of five unsuccessful attempts at reestablishment in the 2000s (Emmel and Daniels, 2006; Daniels, 2009; US Fish and Wildlife Service, 2011; Longcore, 2013).

**Table 2.3**: The year butterfly reintroduction projects were initiated, life-cycle stage at point of reintroduction and quantities released, and whether colonies were subsequently reinforced (key for quantities given: >=over, <=under, ~=approximately).

| Species | Year | Larvae | Pupae | Adult males | Adult females | Total adults | Subsequent reinforcement |
|---|---|---|---|---|---|---|---|
| Apollo | 1908 | 118 | | | | | |
| Apollo | 1912 | 50 | | | | | 150 larvae 'a few years later' |
| large copper | 1914 | | | | | 100> | |
| Adonis blue | 1920 | | | | | >100 | |
| large copper | 1926 | | >500 | | | | |
| large copper | 1927 | | | 25 | 13 | 38 | Annual |
| silver-studded blue | 1942 | | | | | 90 | |
| Glanville fritillary | 1945 | | | | | >100 | |
| black hairstreak | 1952 | | | | | <20 | |
| Glanville fritillary | 1957 | 500 | | | | | |
| ringlet | 1958 | | | | 13 | 13 | |
| marsh fritillary | 1960 | >1,000 | | | | | |
| marbled white | 1964 | | | | 18 | 18 | |
| Glanville fritillary | 1965 | 1,000 | | | | | |
| marsh fritillary | 1965 | >500 | | | | | |
| silver-washed fritillary | 1969 | | | | 38 | 38 | Few (1970-73) |
| wood white | 1969 | | | | 6 | 6 | Few (1970-71) |
| large copper | 1970 | | | 517 | 551 | 1,068 | Annual |
| wood white | 1974 | | | 4 | 5 | 9 | 6 (1976) |
| wood white | 1974 | | | | 3 | 3 | |
| swallowtail | 1975 | | | | | 228 | |
| Duke of Burgundy | 1976 | | 12 | | | | |
| Scotch argus | 1976 | | | | 63 | 63 | |
| wood white | 1976 | | | 6 | 6 | 12 | |
| silver-studded blue | 1978 | | | | 5 | 5 | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| speckled wood | 1980 | 350 | 50 | | | | Many (1981) |
| Adonis blue | 1981 | | | 27 | 39 | 66 | |
| Duke of Burgundy | 1981 | | 35 | | 6 | 6 | 77 (1982) |
| gatekeeper | 1982 | | | 8 | 8 | 16 | |
| marsh fritillary | 1982 | ~500 | | | | | |
| silver-studded blue | 1982 | | | 7 | 15 | 22 | |
| small blue | 1982 | 25 | | | | | |
| small blue | 1982 | 25 | | | | | |
| Adonis blue | 1983 | | | | | ~1,000 | |
| Glanville fritillary | 1983 | >500 | | | | | |
| marsh fritillary | 1983 | <200 | 6 | 2 | 2 | 4 | |
| marsh fritillary | 1983 | >1,000 | | | | | |
| silver-studded blue | 1983 | | | 6 | 6 | 12 | |
| heath fritillary | 1984 | | | 22 | 31 | 53 | |
| silver-washed fritillary | 1987 | | | | | 5 | 6 adults (1988) |
| dusky large blue | 1990 | | | 22 | 48 | 70 | |
| scarce large blue | 1990 | | | 33 | 53 | 86 | |
| Glanville fritillary | 1991 | 72 | | | | | |
| Apollo | 1992 | | 4 | 15 | 9 | 24 | 1,010 adults (1993-95) |
| large blue | 1992 | 281 | | | | | |
| large blue | 1992 | 300 | | | | | |
| northern brown argus | 1993 | | | 11 | 16 | 27 | |
| baton blue | 1994 | | | | 10 | 10 | |
| Schaus' swallowtail | 1995 | | 764 | | | | 500 (1996), 209 (1997) |
| large copper | 1997 | 190 | | | | | |
| wood white | 1997 | | | | | 20 | |
| Karner blue | 1998 | | | | | | 1,617 adults (by 2006), inc. 1,100 pupae (2001-02) |
| small skipper | 1999 | | | ~200 | ~200 | ~400 | ~200 adults (2000) |
| clouded Apollo | 2000 | | | | 40 | 40 | |
| Karner blue | 2000 | | | | | 1,000 | |
| marbled white | 2000 | | | ~250 | ~250 | ~500 | |
| Karner blue | 2001 | | | | | 23 | 70 adults (2002) |
| regal fritillary | 2001 | | | | 7 | | |
| Adonis blue | 2002 | | | | | 50 | 45 adults (2004) |
| Miami blue | 2004 | | | | | | 276 adults and 3,277 larvae (2007-08) + 3,863 individuals (since 2004) |
| pearl-bordered fritillary | 2004 | | | | | 50 | |
| purple emperor | 2004 | | | | | 160 | |
| purple emperor | 2004 | | | | | 50 | |
| purple emperor | 2004 | | | | | 80 | |
| Karner blue | 2005 | | | | | 315 | |
| purple copper | 2005 | 1,260 | | | | | |
| heath fritillary | 2006 | | | | | 1,511 | |
| purple emperor | 2006 | | | | | 20 | |
| Taylor's checkerspot | 2006 | | | | | | >15,000 larvae and >500 adults (since 2006) |
| Glanville fritillary | 2007 | 14* | | | | | *Nests |
| marsh fritillary | 2007 | 42,400 | | | | | |
| silver-studded blue | 2007 | | | 20 | 40 | 60 | |
| Lange's metalmark | 2008 | 30 | | | | 30 | 210 larvae (2009-15); 144 pupae and 41 adults (2012-15) |
| Apollo | 2009 | 1,408 | | | | | 2,879 (2010-11) |
| small pearl-bordered fritillary | 2009 | 500? | | | | | |
| Richmond birdwing | 2010 | | | | | 500 | |
| Adonis blue | 2011 | | ~55 | | | | |
| Duke of Burgundy | 2011 | 91 | | | | 51 | |
| red-dotted Apollo | 2011 | | | | | 20 | 240 adults (2012-15) |
| pearl-bordered fritillary | 2012 | | | 30 | 34 | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Taylor's checkerspot | 2012 | 2,540 | | | | 130 | |
| bay checkerspot | 2013 | ~5,000 | | | | | |
| bay checkerspot | 2013 | ~5,000 | | | | | |
| heath fritillary | 2014 | | | | 18 | 57 | |
| marsh fritillary | 2014 | | | | | 1,300 | |
| regal fritillary | 2014 | 1,112 | | | | | 5,593 larvae (2015) |
| silver-studded blue | 2014 | | | 8 | 45 | 53 | |
| silver-studded blue | 2014 | | | 2 | 5 | 7 | |
| small blue | 2014 | | | | | 40 | 56 adults (2015) |
| Oregon silverspot | 2016 | 450 | | | | | |
| Quino checkerspot | 2016 | 742 | | | | | 6,291 larvae (2017-18) |
| wood white | 2016 | | | 10 | 10 | 20 | |
| wood white | 2016 | | | 10 | 10 | 20 | |
| Oregon silverspot | 2017 | >900 | | | | | |
| small pearl-bordered fritillary | 2017 | 93 | | 73 | 87 | 160 | |
| small pearl-bordered fritillary | 2017 | 69 | | 40 | 49 | 89 | |
| chequered skipper | 2018 | | | 10 | 32 | 42 | 24 adults (2019); 5 adults (2022) |
| grizzled skipper | 2018 | | | | | 10 | 11 adults (2019) |
| Oregon silverspot | 2018 | 500-600 | | | | | |
| pearl-bordered fritillary | 2018 | | | | | 196 | |
| wood white | 2018 | | | 10 | 10 | 20 | |
| Apollo | 2019 | 300 | | 150 | 150 | 300 | |
| false ringlet | 2019 | | 154 | | | | 240 pupae (2021) |
| Apollo | 2020 | | | | | 490 | 2,529 adults and 21,478 larvae (2021-22) |
| large heath | 2020 | | 45 | | | | |
| Taylor's checkerspot | 2020 | 400 | | | | | |
| yellowish sedge-skipper | 2020 | | | | | 100 | |
| bay checkerspot | 2021 | 3,630 | | | | | 3,859 larvae (2021) |
| mottled duskywing | 2021 | | | | | 700 | |

As well as larvae, large numbers of adult butterflies were used to reinforce colonies in several cases. The recent LIFE Apollo2020 project released 2,529 adult and 21,478 *P. apollo* larvae between 2020-21 at Kruczy Kamień Reserve, Chojnik Mountain, and Karkonosze National Park in Poland, which followed on from Karkonosze National Park's release of 300 adults and 300 larvae at Kruczy Kamień in 2019 (European Commission, 2021). In North America, over 15,000 larvae and 500 adult Taylor's checkerspot *E. e. taylori* butterflies were released across South Puget Sound, Washington between 2006-12 as part of a Washington Department of Fish and Wildlife (WDFW) partnership project to reestablish the species on historical prairie in the state (Linders 2011, 2012; WDFW, 2013). At the other end of the spectrum, species were reintroduced using founder populations as small as 10 adult females, such as in southeast Finland for the successful reestablishment of the baton blue *Pseudophilotes baton schiffermuelleri* in 1994 (Marttila, 1997). That same year, a wood white *Leptidea sinapis* colony was successfully reintroduced to Warwickshire, England using only 20 adult butterflies as part of a clandestine release (M. Slater, personal communication).

Total reintroduction projects initiated annually was found to have increased since the 1990s (Figure 2.1). On average, 3.7 reintroductions were attempted per year in the 1980s, 3.2 in the 1990s, 5.5 in the 2000s, and 7.2 in the 2010s. A peak of 13 projects was reached in 2014 before numbers declined to between six and eight projects annually from 2015-18. The fall in projects thereafter was possibly due to fewer organisations declaring or publishing outcomes given the short timeframe between then and now (autumn 2022) and project delays, postponements, or cancellations caused by the coronavirus disease 2019 (COVID-19) pandemic.

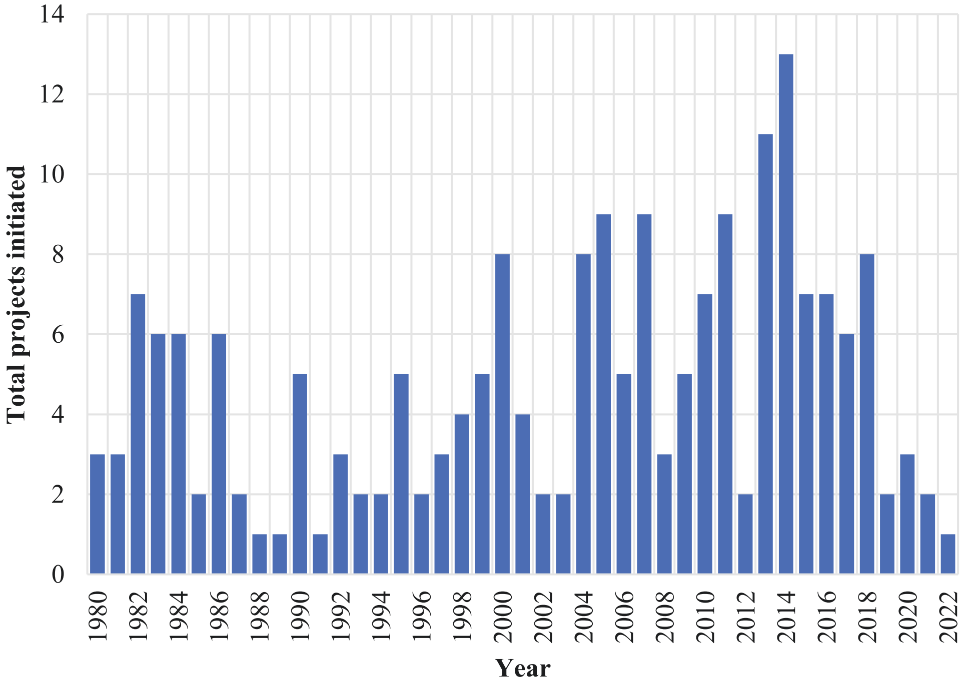

**Figure 2.1**: The number of reintroduction projects initiated globally from 1980 onwards. Note that a minimum of six projects are initiated per year between 2013-18, with a peak of 13 projects in 2014.

## 2.4 Discussion

Reintroductions are necessary for rare, endangered, or at-risk butterflies to reverse extirpation and compensate for losses induced by a wide range of environmental and anthropogenic drivers of decline globally. However, only 128 (24.3%) of cases covered by this review have definitively resulted in the reestablishment of reintroduced species – a value outnumbered by the quantity which have failed in either the short or long-term (220; 41.8%). Williamson and Fitter (1996a, 1996b) propose the ‘tens’ rule, which suggests that invasive species have a success probability of around 10% in each of three invasion stages (escaping, establishing, and becoming a pest) in non-native environments. For butterflies reintroduced to sites in their native range, the probability of reestablishment indicated by the results of this study (24.3%) is over twice that of invasive species. The desired outcome of a butterfly reintroduction is difficult to achieve, and the challenges faced by projects great in number.

### 2.4.1 Challenges Facing Reviews of Butterfly Reintroductions

Oates and Warren (1990) state that their review of butterfly reintroductions (and ours) is believed to be "an enormous underestimate of the true situation and represents only a tip of the iceberg." Research on one species in one country by Witkowski *et al.* (1997) – *P. apollo* in Poland – gives the impression that the number of uncollated historic butterfly reintroductions in mainland Europe may outnumber those documented in the UK and Ireland by many orders of magnitude. Oates and Warren (1990) estimate that the all-time tally of attempts at reestablishment in the UK and Ireland alone involves "at least a four-figure sum." The 577 cases that we present here is clearly an underestimate of the true number of naïve releases and genuine attempts at reestablishment that have taken place globally, given the practice of reintroducing butterflies in a clandestine fashion has been a part of butterfly culture for nearly two centuries, long before the ecological requirements of butterflies was well understood and the dawn of reintroduction and metapopulation biology (e.g. Frohawk, 1934; Thomas, 1984; Collier, 1978; Hanksi and Gilpin, 1997; Dincă *et al.*, 2018; Maes *et al.*, 2019).

We have added 139 cases of global and post-2019 UK and Ireland reintroductions to existing Butterfly Conservation (114 cases) and JCCBI (270 cases) research using desk-based methods suitable for broad data aggregation. Our approach has highlighted the importance of direct communication with project staff and stakeholders in order to obtain detailed information on the status of cases and perceived successes and failures of projects. This is illustrated by the paucity of published research available online following the attempted reestablishment of Schaus' swallowtail *Papilio aristodemus* to the Florida Keys between 1995-99 (Emmel *et al.*, 1998). An article in *USGA Turfgrass and Environmental Research Online* (Daniels and Emmel, 2004) – from where some data were retrieved for this review – only summarises the project's scope, not its outcomes or challenges.

A 2014 interview with the captive breeding project's director, Thomas Emmel, reveals that releases were met with initial resistance from landowners, funding from the US Fish and Wildlife Service (USFWS) was withdrawn in 1999, and drought years followed, which led to a dramatic decline in abundance (Braverman, 2009). No *P. aristodemus* were found in 2012 after emergency authorisation was granted to collect and captively breed individuals, and the seven cases have therefore been interpreted in this study as long-term failures. Similar insight (in absence of evidence such as published reports and peer-reviewed journal articles) is not available for a vast majority of reintroduction projects. On behalf of Butterfly Conservation, Dr Kate Dent used personal communications to obtain data about many clandestine and officially sanctioned releases in the UK and Ireland. This was made possible thanks to a strong network of experienced staff, branch committee members, external contacts, and partner organisations such as Natural England.

### 2.4.2 Post-Release Monitoring and Population Health

The challenges faced by in-progress reintroductions are numerous, however follow-up research is essential to determine colony status and contribute to global knowledge of best practice. Post-release work should not be limited to logistics and methodology – it must also encompass biological assessments and regular monitoring of reestablished populations. An example of good practice is the 1992 reintroduction of *P. apollo* to the Pieniny Mountains in Poland, which saw a founder population of 52 butterflies reinforced by 1,010 adults from 1993-95 (Witkowski and Adamski 1996; Witkowski, 1997). Although successful, deformation or reduction of wings occurred in a large number of individuals in the isolated population, which was restituted from a small stock of founders (Adamski and Witkowski, 1999).

Various mutations have been reported in *P. apollo* from other sites, but none of them resulted in phenotypes such as those found in malformed individuals from the Pieniny Mountains (Descimon, 1988; Pierrat and Descimon, 2011; Łukasiewicz *et al*., 2016). DNA cloning and sequencing suggested a genetic mutation (a lesion in the *wg* gene) inherited from the small number of butterflies reintroduced to Pieniny. Reintroduced populations must, therefore, be subject to ongoing monitoring for morphological variance as well as apparent health to identify whether deleterious alleles and environmental factors may eventually lead to extirpation, particularly in the case of isolated colonies.

The recent Butterfly Conservation reintroduction of *C. palaemon* to Rockingham Forest in England (2018-) has been subject to strict biosecurity and post-release health surveillance (PRHS) protocols, which were developed in collaboration with the Disease Risk Analysis and Health Surveillance (DRAHS) team at the Zoological Society of London (ZSL). The objectives of the ongoing programme are to prevent the introduction of alien infectious agents to reintroduction sites in England, monitor the health of adult *C. palaemon* throughout translocation, and detect disease hazards (Jaffe and Sainsbury, 2017, 2019; Donald and Sainsbury, 2018; Shadbolt and Sainsbury, 2020a, 2021) (Figure 2.2). Stock was sourced from a number of geographically distinct sites across the Fagne-Famenne region of Belgium for reintroductions in 2018, 2019, and 2022 to ensure sufficient genetic diversity in founder colonies. In conjunction with disease risk management (DRM) and PRHS, the reintroduced *C. palaemon* population is better protected against enhanced genetic drift load, disease outbreaks, and parasites which may be translocated with host species (e.g. Gompper and Williams, 1998; Pizzi, 2009; Mattila, 2012; Willi *et al*., 2013). The project's DRM and PRHS protocols are based on previous ZSL health monitoring protocols and guidelines for invertebrate translocations (Invertebrate Link, 2010;

Colvile and Sainsbury, 2012; Vaughan-Higgins *et al.*, 2015; Shadbolt and Sainsbury; 2020b, 2020c) but are specific to butterflies, and should be adopted by future reintroduction projects.

**Figure 2.2**: Tony Sainsbury (Zoological Society of London) of the Disease Risk Analysis and Health Surveillance (DRAHS) team carrying out pre-release health examinations of translocated Belgian *C. palaemon* at Fineshade Wood.

## 2.4.3 Notable Reintroductions

Some projects do not have time to develop rigorous methodology in advance of initiation, however. This was the case for the 2004 emergency relocation of *P. spinifera* near Lidsdale, Australia. A New South Wales Roads and Traffic Authority (RTA) *Review of Environmental Factors* (2002) failed to detect the presence of the nationally threatened butterfly during a survey for a road realignment project in the Central Tablelands. Once alerted to the population, the RTA prepared and implemented a butterfly management programme, which partly involved translocating larvae from the road's footprint to compensatory habitat using novel methods (Mjadwesch 2004a, 2004b; Mjadwesch and Nally, 2004; Mjadwesch, 2008). A team from Conservation Volunteers America (CVA) planted 177 potted blackthorn *Prunus spinosa* ssp. *lasiophylla* hostplants from a community nursery throughout Neubecks Hill habitat that had already been cleared of vegetation. Attendant ants were attracted to the *P. spinosa* bridging habitat using sugar and honey solutions in two-thirds of cases, as it is thought female *P. spinifera* egg-laying site selection is related to pheromone signals arising from the presence of ants

(Mjadwesch, 2008). A total of 54 of 177 potted *P. spinosa* plants were utilised by *P. spinifera* larvae. With the support of National Parks and Wildlife Service volunteers and RTA staff, a total of 1,260 larvae were transferred in 12 nights to preserved Neubecks Hill habitat. This account of butterfly translocation in the face of anthropogenic pressures such as development is a novel example of reactive conservation that may benefit threatened butterfly populations with similar ecological requirements.

Climatological factors such as extreme weather events can also negatively influence results. Repeated attempts to reestablish *C. t. bethunebakeri* in the Florida Keys have been undermined by major hurricanes, most recently Irma in 2017. Researchers have begun to favour captive rearing given the vulnerability of populations to extirpation due to the short-term threat posed by hurricanes (e.g. Emmel and Daniels, 2003, 2009; Minno and Minno 2009; Glassberg and Olle, 2010; Olle, 2010; Halupa, 2012; Longcore, 2013). Even if reintroductions are well documented, methods may need to be adjusted periodically in response to the growing impact of climate change (Cannon *et al*., 2010).

Robust research is the foundation of any successful project. The first reintroduction of the large blue *Phengaris arion* to Devon, England in 1983 after the species' extirpation in 1979 was underpinned by years of preparation. Delivered by partnerships between the Large Blue Committee (LBC), the Centre for Ecology and Hydrology (UKCEH), Natural England, Butterfly Conservation, and the University of Oxford, releases have now taken place at 16 sites since 1983. A total of eight out of sixteen cases have resulted in colony establishment, with one too soon to judge (as of 2019). The 50.0% success rate of *P. arion* cases headed by the LBC and its collaborators is over double the global average for all butterfly species of 22.2%. A 1992 reintroduction to Green Down at Polden Hills in Somerset – founded by 281 larvae translocated from Sweden – is now home to the largest *P. arion* colony in the world. The wealth of peer-reviewed scientific evidence available on *P. arion* has benefitted conservation efforts by improving understanding of the butterfly's ecology in the UK and mainland Europe (e.g. Thomas, 1995; Thomas *et al.*, 1997; Thomas, 2002; Settele *et al.*, 2012). Successful conservation in the UK led to the IUCN downgrading the status of *P. arion* from Vulnerable to Near Threatened in 1996 (Thomas *et al.*, 2009, 2011).

Research on the 1990 reintroduction of the scarce large blue *P. teleius* and dusky large blue *P. nausithous* to Moerputten nature reserve in the Netherlands references Thomas *et al*.'s work on *Phengaris* spp. (Wynhoff, 1998). The project was executed in accordance with criteria outlined in the Invertebrate Link's code of conservation practice for invertebrate translocations (Invertebrate Link, 1986) and the Dutch Butterfly Protection Program (Ministry of Agriculture, Nature Conservation and Fisheries, 1989). Populations of both butterflies were monitored from 1990-96 and reestablishment achieved. Research continues at Moerputten, most recently into hostplant translocation to restored wet meadows to encourage the spread of *Myrmica* ant colonies (Sevilleja, 2021). Wynhoff (1998) does not consider the number of years populations are able to persist after reintroduction to be a reliable indicator of success, however, given high mortality can occur as a result of environmental pressures such as bad weather (Thomas, 1995). Nonetheless, peer-reviewed research of successful cases such as this add to the canon of best practice in reintroduction biology.

## 2.5 Conclusions

That only 24.3% of known global cases have resulted in reestablishment is a clear indication of the scale of the challenge faced by those tasked with reintroducing butterfly species. Wynhoff (1998) correctly states that, although reintroductions give the appearance of an easy-to-handle tool in nature conservation, success is not guaranteed. Even if methodology is sound and habitats have been restored in accordance with species' ecological requirements, environmental pressures can wipe out fragile founder populations and lead to failure. An increase in unforeseeable extreme weather events such as prolonged droughts and flash-flooding (as the UK experienced in 2022) will heap additional pressure on reintroductions. This may necessitate an increase in colony reinforcement or complementary captive rearing programmes to insure projects against climatological variables.

The accuracy of findings in this review hinge on the availability (and accessibility) of data. Desk-based studies are fast and inexpensive and may be the only viable approach in resource-limited situations, but have shortcomings. If data on reintroductions have not been published or collated, there is a higher probability of mistakes being unknowingly duplicated due to poor understanding of best practice. Only two published systematic reviews of butterfly reintroductions involving personal communications with project directors and stakeholders are known to exist – by Oates and Warren (1990) (with an update by Pullin, 1996) and Schultz *et al.* (2008). However, even these are limited in scope and do not incorporate global efforts.

Given the speed of development in the field of reintroduction biology and increase in the number of projects that have been initiated since publication of Schultz *et al.*'s 2008 review (83 total), it is essential that collective knowledge of best practice and the status of butterfly reintroductions keeps pace. Some data featured in this review were obtained from non-scientific sources such as news articles due to an absence of peer-reviewed research, progress reports, and summaries. Systematic documentation of cases and open-access publication of results is essential in order for researchers to review outcomes and project coordinators to develop effective methodology that builds on prior success.

To bring global reintroduction biology together, a major research project to determine the true extent of sanctioned reintroductions and approximate the number of clandestine attempts is necessary in order to communicate project takeaways and best practice to a wider international scientific audience. A synopsis of reintroduction and translocation actions, similar to a recent compilation of the effects of interventions for butterflies and moths (Bladon *et al*., 2022), is recommended. A revised Invertebrate Link record of insect establishment form should be digitally circulated to major conservation organisations and relevant government departments globally in order to reduce the necessity of direct communication. Regional volunteers should be recruited to assist with this process and circulate calls for data amongst potential sources and submit data to a central depository for processing. A more accurate picture of both sanctioned and clandestine reintroductions will enhance and standardise best practice globally and complement the translocation recommendations made by Daniels *et al*. (2018, 2020). As ever, but particularly in the case of reintroductions, learning from the past will better inform the future of butterfly conservation.

# 3

# The Value of Museum and Other Uncollated Data in Reconstructing the Decline of the Chequered Skipper Butterfly *Carterocephalus palaemon* (Pallas, 1771)

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## Abstract

The chequered skipper butterfly *Carterocephalus palaemon* (Pallas, 1771) was declared extinct in England in 1976 after declining precipitously in range and abundance during the 20th century. By searching and collating museum and other records, we show how a deeper understanding of this decline can be achieved, thus furthering conservation objectives. A preexisting Butterflies for the New Millennium (BNM) database of United Kingdom butterfly species records, created by Butterfly Conservation in conjunction with the Biological Records Centre (BRC), contained 266 historic *C. palaemon* records from England. United Kingdom (UK) museums and natural history societies were contacted for specimen data, and these sources added 2,175 new records to the BNM. Owners of private specimens were also contacted, which accounted for a further 465 records. Specimens originating from

UK museums, other institutions, and private collections represent 2,640 (74.7%) of total new records. Other sources, such as personal accounts held in museums, published and unpublished texts produced an additional 894 records. A further 437 records from museums, private collections, and other sources were considered partial and omitted from the data due to limited or misleading date and/or locality information. In summary, data from UK museums and other sources has infilled English *C. palaemon* distribution prior to 1976, offering further insight into potential environmental and anthropogenic drivers of decline at key sites. The quality and quantity of data obtained using the method outlined in this study suggests similar work could be carried out for other extinct or declining butterfly species to improve knowledge of habitat requirements and historical distribution via modelling, identify causes of decline, and provide valuable information for potential reintroductions.

## 3.1 Introduction

In order to reconstruct the historic decline of a butterfly species, long-term data must be collected to understand the extent to which various environmental and anthropogenic drivers may have affected its abundance and distribution. Although there is a growing body of literature on the value of museum specimens for conservation of many different species (e.g. Roy *et al.*, 1994; Shaffer *et al.*, 1997; McCarthy, 1998; Krupnick and Kress, 2005; Bálint and Katona, 2013; Nakahama, 2021), museums have been underutilised as sources of information for declining or extirpated butterflies such as *C. palaemon* (Dockerty and Cook, 2020; Nakahama, 2021). *C. palaemon* was declared extirpated in England in 1976 after undergoing a precipitous decline in the 20th century, caused by factors such as coppice abandonment, agricultural intensification, and coniferisation (Collier, 1986; Warren, 1990; Ravenscroft, 1995; Moore, 2004). Despite being a prominent case of an insect going nationally extinct, the decline of *C. palaemon* in England is not well documented despite studies by Collier (1966, 1984), Farrell (1973), Ravenscroft (1995), and Moore (2004) due to a paucity of hard data. In order to understand how a restricted but once locally abundant butterfly could be lost, a research collaboration between the University of Northampton and Butterfly Conservation to complement the reintroduction of *C. palaemon* to Rockingham Forest in England was established to collect historic *C. palaemon* date and locality information from museum and private collections, personal accounts, and other sources of uncollated data.

## 3.2 Methods

### 3.2.1 Data Collection

A message requesting historic English *C. palaemon* records from institutions and private collectors was published on the Natural Sciences Collection Association (NatSCA) JiscMail discussion list (natsca@jiscmail.com) (Jisc, 2021). *C. palaemon* specimens listed for sale were located on eBay (2021), and sellers contacted via private message to request data. A blog post, presentation to the general public, and social media posts were also used (Wildman, 2020, 2021a, 2021b). Every attempt was made to verify the authenticity and source of records and eliminate duplicates. Time and locality data from specimen labels were interpreted as records of sightings. For textual accounts, where abundance of *C. palaemon* was unable to be precisely quantified (e.g. a diary entry stated that "quite a number of chequered skippers" were at Wakerley Wood in 1947 [Bates, *c*. 1945-50]), a single record was included to indicate presence to avoid overestimation. Historical abundance at many sites was likely underestimated as a result (see Farrell, 1973).

Data from museums and private collections were provided in the form of photographs, spreadsheets, and scans of record cards. Label data were transcribed from photographs and record card scans remotely by the lead author, museum staff, or, in the case of a private Wiltshire collection, volunteers acting under instruction. Museums were emailed to inquire whether they held *C. palaemon* specimens. Data were sourced from private, unpublished sources (e.g. Dale, *c*. 1810-30; Bates, *c*. 1945-50), published sources (e.g. Ryland *et al*., 1902; Macqueen, 1969; Archer-Lock, 1982; Duddington and Johnson, 1983), local researchers, butterfly collectors, and museums. Data were obtained from 40 UK institutions (including museums, collections centres, natural history societies, universities, and trusts) and one US museum. Where collected museum or other uncollated data duplicated existing BNM records, they were omitted from this study.

### 3.2.2 Dataset Creation

A worksheet was created to which all records meeting quality control criteria were added. Each record was assigned a unique identification number to avoid confusion with other records and duplication. Columns were given the following headings and completed for each record: decade, date (dd/mm/yyyy), county of origin, vice county number, nearest known locality, Ordnance Survey (OS) grid reference, type and source of record (MS=museum specimen, PS=private specimen, UP=unpublished text, PU=published text, ED=existing data), present location of data, recorder name, collector name, reference (if from a textual source), museum collection name, and notes.

Northamptonshire and Cambridgeshire localities were assigned 6-figure OS grid references (10-figure for small sites) based on Northamptonshire Site Register (D. James, personal communication) and Bird Club Gazeteer (Cambridgeshire Bird Club, 2021) lists, respectively.

Butterflies for the New Millennium (BNM) – a butterfly recording scheme organised by Butterfly Conservation and the Biological Records Centre (BRC) in the UK, and the Dublin Naturalists' Field Club in the Republic of Ireland – was developed in 1995-99 to assess the status of all native species for *The Millennium Atlas of Butterflies in Britain and Ireland* (Asher *et al*., 2001). Historical records dating back to the 17th century and records collated by the BRC for a previous atlas (Heath *et al*., 1984) were incorporated. Since 1995, it has operated as the UK recording scheme for distributional casual records and now holds over 14 million records (Butterfly Conservation, 2021). These data have been used in over 50 scientific research papers (e.g. Warren *et al*., 2001; Thomas *et al*., 2004; Suggitt *et al.,* 2018), and as part of a longstanding series of State of Butterflies reports (Fox *et al*., 2007, 2011, 2015). Grid references for localities elsewhere in England were generated using the UK Grid Reference Finder website (UK Grid Reference Finder, 2021) in cases where records lacked existing geographic coordinates. Additional columns were later added to the database to account for changes in sites names, records being assigned to localities in different counties, and grid reference irregularities versus raw data.

### 3.2.3 Data Classification

Lynne Farrell's JCCBI report on the status of *C. palaemon* in England (Farrell, 1973) was classified as a published text for the purpose of this analysis to differentiate it from personal accounts such as diaries. Even though the report is not in the public domain, it was printed and circulated amongst JCCBI member organisations after its completion in September 1973. Diaries held in museums were classified as unpublished texts, the same as accounts in private notebooks (M. Fuller, personal communication; A. Russell, personal communication).

### 3.2.4 Criteria for Inclusion and Exclusion of Data

Records were considered to have met quality control criteria and deemed complete if they contained date and locality information (e.g. a place name) and originated from England. Naming variations (e.g. checkered skipper, *Papilio paniscus* (Fabricius, 1775)) were also permitted. Records were excluded from analysis if the provenance of a label could not be determined (e.g. one specimen was vaguely labelled 'Morris Links'). Specimens labelled with settlement names (e.g. Corby) were assigned to bestcandidate woodland in close proximity using georeferenced historical OS maps (National Library of Scotland, 2022) if the site met the following criteria: a) was >10ha in size (equal to the smallest known historically occupied site in England, Barrowden Fox Covert, 10.2ha), b) possessed internal ride structure, and c) was not wholly coniferous. If clear and obvious provenance of a specimen could not be determined, however, its locality was not changed. Original label wording was often left unaltered to limit the impact of speculation and personal bias on records.

Ambiguous specimen labelling was a common practice historically, and often a consequence of the commercial interests of professional dealers outweighing their interest in accuracy (D. Green, personal communication). Solitary records from outside the accepted geographic range of the species (Rockingham Forest and Lincolnshire) were accepted to illustrate the stated locality of all records, but treated with caution (Blathwayt, 1925; Turner, 1955; Mendel and Piotrowski, 1986; M. Fuller, personal communication), as eggs and larvae collected from well-known colonies could have instead been labelled with their breeding and/or release location (D. Green, personal communication). Several collectors were resident in Kent, Somerset, Buckinghamshire, and West Sussex around the time period specimens are dated: Edgar James Hare (1884-1969) in London and Kent, William Holland Ballett Fletcher (1852-1941) in West Sussex, Archdale Palmer Wickham (1835-1935) in Somerset, and Cyril Humphrey Cripps (mid-20th century) in Buckinghamshire. Wild-caught and captive-bred specimens could also be purchased from commercial dealers, particularly in the late 1800s-early 1900s (Allan, 1943; Salmon *et al.*, 2000; M. Fuller, personal communication). Such records could be interpreted as hoaxes, cases of misidentification, or unsanctioned releases following captive breeding/rearing or translocation. Partial records (lacking either year or site) were omitted from the dataset.

### 3.2.5 Data Visualisation

Plots were created in Microsoft Excel (Microsoft Corporation, 2021) and the dataset exported to Quantum Geographic Information System (QGIS) (QGIS Development Team, 2021) as a .csv file for mapping. The Field Studies Council (FSC) Biological Records Tool (Field Studies Council, 2022) was used to import records and plot them as monads on an OS Boundary-Line vector layer (Ordnance Survey, 2022) with a GADM (Database of Global Administrative Areas) administrative boundary line inset (GADM, 2018).

# 3.3 Results

## 3.3.1 Summary of New Data

Museums and natural history society specimens that met quality control criteria provided 2,175 new English *C. palaemon* records. Specimens in private collections accounted for a further 465 new records. Specimens originating from museums, other institutions, and private collections represented 2,640 (74.7%) of total records. Other sources, such as personal accounts held in museums, published and unpublished texts produced an additional 893 records. A further 437 records from museums, private collections, and other sources did not meet quality control criteria and were omitted from the dataset due to limited or misleading date and/or locality information. Incomplete records that did not meet quality control criteria have been retained for future reference, as it is possible the provenance of some specimens could eventually be determined using new information.

The existing BNM database contained 266 records. A total of 3,534 new records were collected through this project (a 1328.6% increase in known records) (Figure 3.1). UK museum data were principally dated between 1880-1959 (2112 records), with 1940-49 being the most abundant decade (949 records). Only 39 museum records were dated between 1826 (the oldest specimen) and 1879. The most recent museum specimen was from Monks Wood, Huntingdonshire, collected on the 25th May 1965. Only 24 museum specimens were dated between 1960 and 1976, whereas 285 records belonging to the same time period were obtained from published and unpublished texts (e.g. Collier, 1966; Macqueen, 1969; Farrell, 1973; M. Fuller, personal communication) (Figure 3.2).

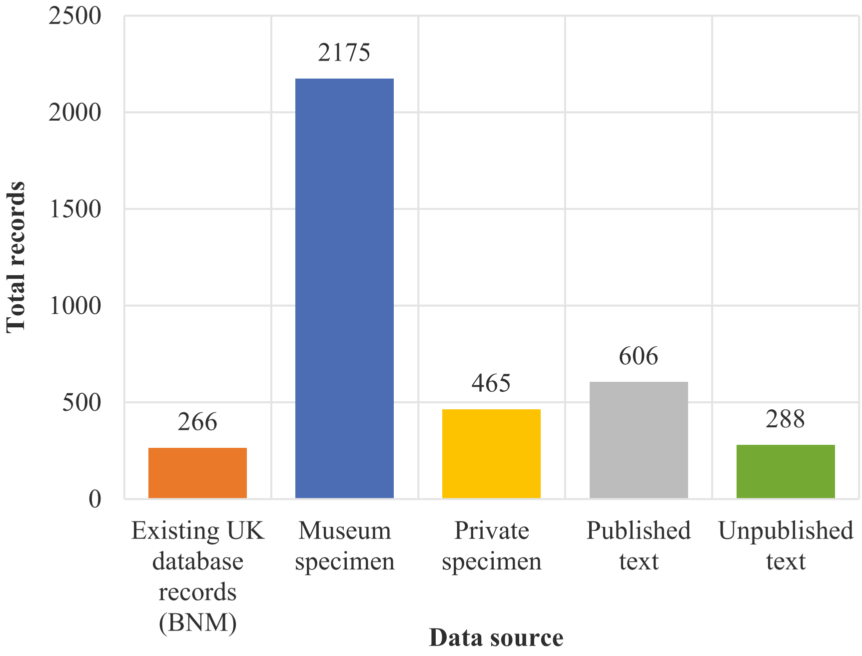


**Figure 3.1**: The number of historic English *C. palaeomon* records by data source. Note the quantity of records collected from museum specimens compared to existing Butterflies for the New Millennium (BNM) records.

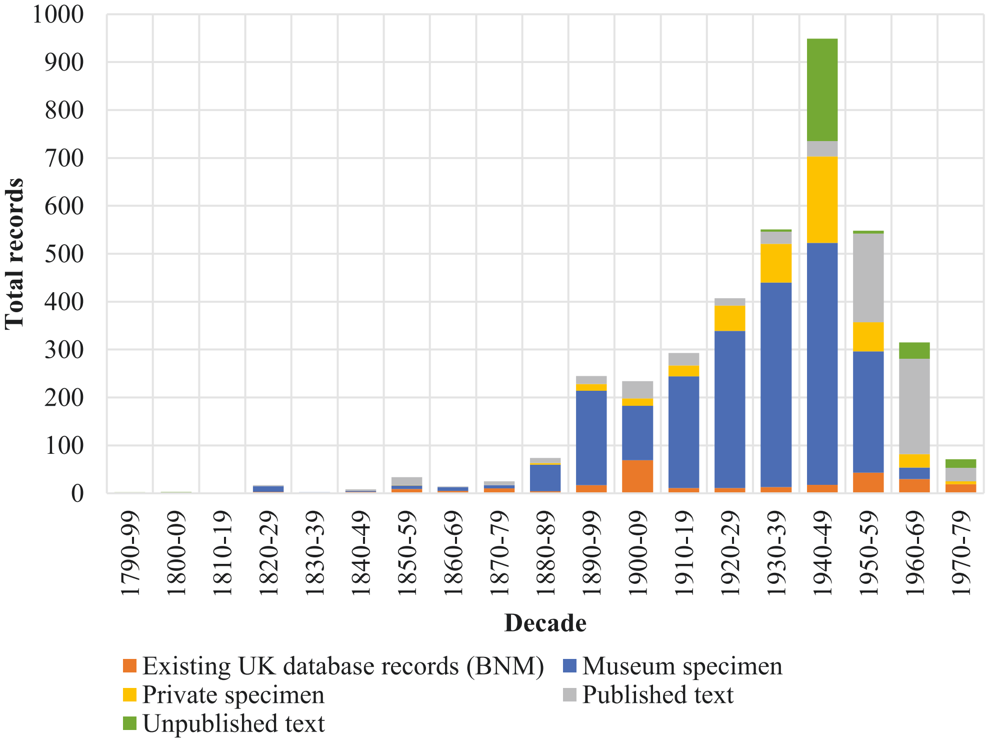


**Figure 3.2**: The total number of historic English *C. palaemon* records by decade from all data sources. Note the contribution made by published and unpublished texts such as reports and entomological diaries from the 1940s onwards.

A total of 803 UK museum and natural history society specimens were taken from Cambridgeshire (748 specimens) and Huntingdonshire (55 specimens) (63.9% of total records from both vice-counties combined), 250 (59.1%) from South Lincolnshire, and 924 (57.5%) from Northamptonshire. In total, 1,978 museum specimens belonged to these four vice-counties. The Natural History Museum, London (NHM) donated the largest number of complete records (681), alongside 92 incomplete records (Table 3.1). Magdalene College, Cambridge held 229 records, 213 of which were from Fermyn Woods in Northamptonshire. Peterborough Museum and Art Gallery, Bristol City Museum and Art Gallery, Brighton Museum and Art Gallery, Oxford University Museum of Natural History, and the University Museum of Zoology, Cambridge (UMZC) provided >100 specimens each. Lancashire and Cheshire Entomological Society data (21 records) were held by National Museums Liverpool. Both Wisbech and Fenland Museum (60 records) and Magdalene College, Cambridge data were supplied by the UMZC.

Only one specimen held in a private collection originated from a Rutland site, whereas 39 were from museum collections. Similarly, only 17 South Lincolnshire specimens were held in private collections, compared to 250 in museums. Records originating from Kent, Devon, Dorset, Hampshire, Leicestershire (distinct from Rutland, the location of the Luffenham Heath sub-landscape near Barrowden and Wakerley Woods), Norfolk, and Oxfordshire were obtained from museums, but these vice-counties were not represented in any private collections. Specimen data from Derbyshire and Worcestershire (three records total) were the only vice-counties represented by private collections not known to be present in any museum collections.

**Table 3.1**: The number of labelled English *C. palaemon* specimens per museum and natural history society that met quality control criteria for inclusion in this chapter.

| Institution | Specimens meeting criteria |
|---|---|
| Natural History Museum, London | 681 |
| Magdalene College, Cambridge | 229 |
| Peterborough Museum and Art Gallery | 151 |
| Bristol City Museums and Art Gallery | 148 |
| Brighton Museum and Art Gallery | 130 |
| Oxford University Museum of Natural History | 123 |
| University Museum of Zoology, Cambridge | 113 |
| National Museums Liverpool | 86 |
| Wisbech and Fenland Museum | 60 |
| Royal Albert Memorial Museum, Exeter | 54 |
| Manchester Museum | 51 |
| Chelmsford and Essex Museum | 42 |
| Sheffield City Museum and Mappin Art Gallery | 34 |
| Birmingham Museum and Art Gallery | 22 |
| Lancashire and Cheshire Entomological Society | 21 |
| Potteries Museum and Art Gallery, Stoke-on-Trent | 20 |
| Plymouth City Museum and Art Gallery | 18 |
| Museum of Reading | 16 |
| Northamptonshire Natural History Society | 16 |
| Leicester City Museums' Service | 16 |
| Tolston Museum, Huddersfield | 11 |
| Hampshire Cultural Trust | 10 |
| Bolton Museum and Archive Service | 10 |
| Hull City Museums and Art Galleries | 10 |
| Glasgow Museums | 10 |
| Saffron Walden Museum | 8 |
| Dorset County Museum | 8 |
| Leeds Museums and Galleries | 7 |
| Cliffe Castle Museum, Keighley | 6 |
| Warwickshire Museum Service | 5 |
| Hampshire County Museums Service | 4 |
| Yale Peabody Museum | 4 |
| Portsmouth Museums and Records Service | 3 |
| Bedford Museum | 2 |
| Natural History Museum, Nottingham | 2 |
| Gallery Oldham | 1 |
| Herbert Art Gallery and Museum, Coventry | 1 |

BNM data were dwarfed by new data at all major English sites. New data confirmed the importance of the Rockingham Forest landscape by infilling known distribution (Figure 3.3). Data from museum specimens pushed back the earliest record year at nine of the 20 most populous English sites. In the case of Great Fen (under which Holme and Woodwalton Fen records were merged), the earliest dated museum specimen attributed to Holme Fen was 1851, whereas the earliest existing BNM record attributed to Woodwalton Fen was 1950. This accounted for the 99-year difference in earliest record year (Figure 3.4). The vice-counties of Derbyshire and Kent, and 31 English localities with more than one record were not represented in existing BNM data.

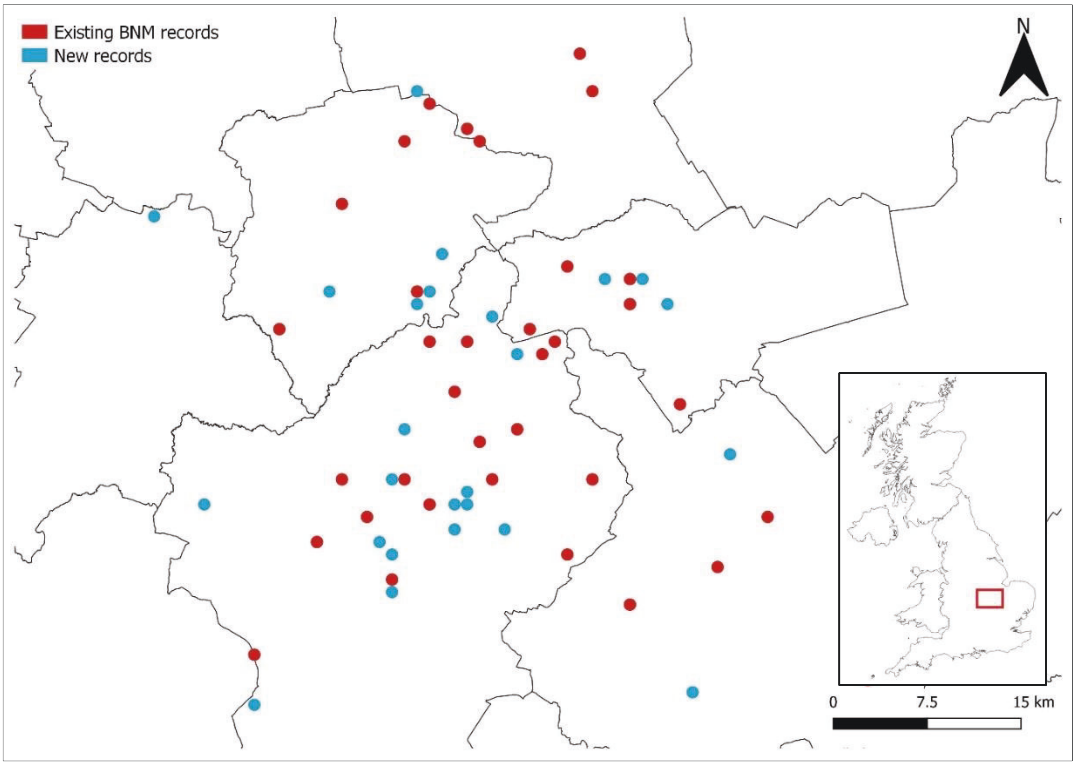


**Figure 3.3**: *C. palaemon* monads of existing Butterflies for the New Millennium (BNM) records and new records to indicate historic presence in Rockingham Forest and the Midlands, 1798-1976. Presence is concentrated in North Northamptonshire, Rutland, and west of Peterborough in the Castor Hanglands area.

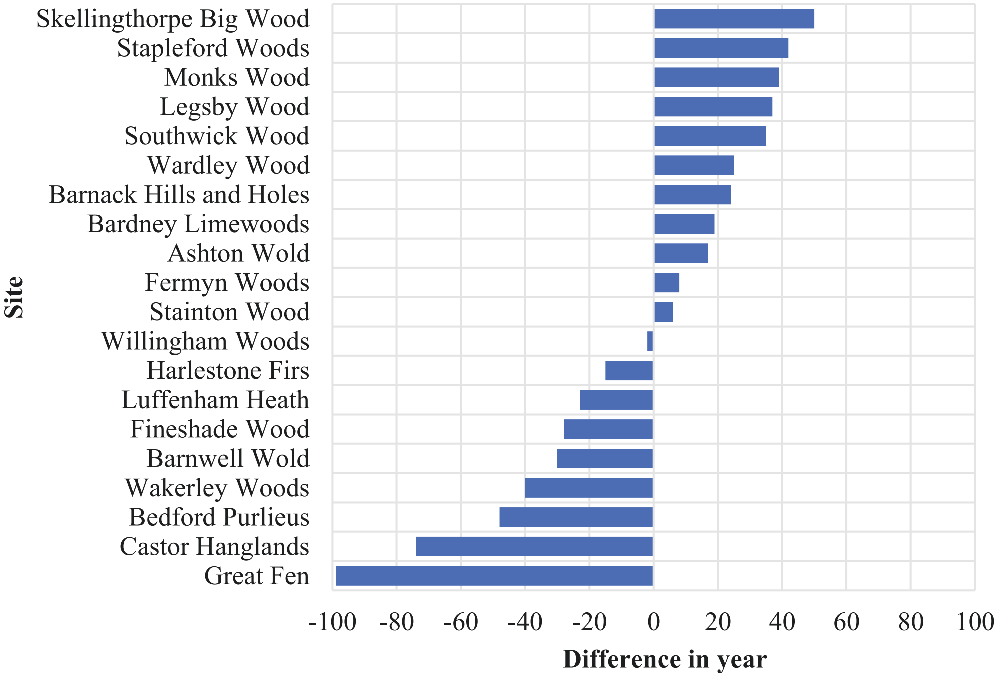


**Figure 3.4**: The difference in earliest record year for new *C. palaemon* museum specimens versus existing Butterflies for the New Millennium (BNM) data at the 20 most abundant English sites.

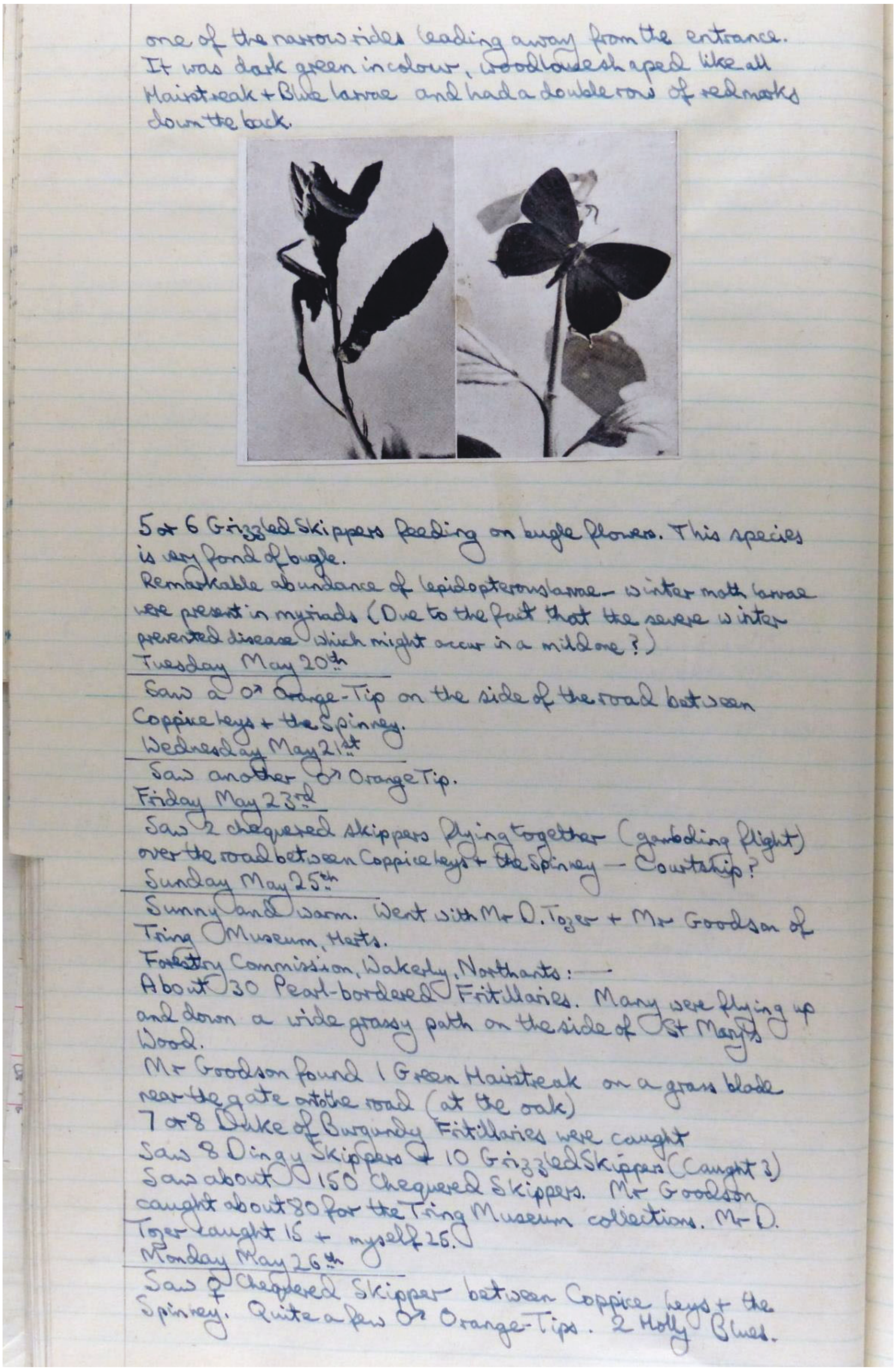
Only two museum specimens meeting quality control standards were dated later than 1964 (both 1965). One is housed at the NHM (BMNH(E): 1381012), and the other at the Royal Albert Memorial Museum, Exeter (RAMM). The NHM specimen, labelled 'G A. M' from Collyweston Great Wood and Eastern Hornstocks is one of only two museum specimens from the site. The RAMM specimen (EXEMS: 74/2015/213) was captured at Monks Wood in Huntingdonshire. Three newer specimens dated 1967-69 did not meet quality control criteria as their provenance could not be determined. Of 14 total museum specimens from 1964, one was from the NHM and labelled Wigsley Wood – a Nottinghamshire site west-southwest of Skellingthorpe Woods in South Lincolnshire. This 'A. Palmer' specimen (BMNH(E): 1363871) was the only Wigsley Wood and post-1939 Nottinghamshire record with definitive provenance collected during this study (a single 1960 private specimen was vaguely labelled Nottingham). J.C. Dale manuscripts at the Oxford University Museum of Natural History pushed back the earliest English *C. palaemon* record by five years to 1798 (Clapham Park Woods, Bedfordshire) compared to BNM data (Gamlingay Wood, Cambridgeshire, 1803).

## 3.3.2 Butterfly Collecting at Fermyn Woods and Wakerley Woods

Cyril Humphrey Cripps and S.W. Humphrey (forename unknown) collected a combined total of 283 *C. palaemon* at Fermyn Woods between 1942-44. Magdalene College donated 213 records (all Cripps) from the site. A single private Wiltshire collection included 70 Humphrey specimens. Sidney H. Kershaw was named as the collector of 13 additional specimens belonging to the same private collection. A total of 41 specimens dated 1940 are unlabelled but considered to have almost certainly been captured by Kershaw because of the characteristic way they are badly set (S. Clarke, personal communication). Cripps, Humphrey, and Kershaw's specimens (including unlabelled attributions) accounted for 77% of all records from Fermyn Woods (437). Overall, 136 new Fermyn records were from the private Wiltshire collection, and 268 from museum collections, emphasising the historical significance of the woodland complex in respect to the wider Rockingham Forest landscape. Existing BNM data contained only 10 records attributed to Fermyn.

Cripps, who had an interest in rarer butterflies (St John's College obituaries, 2000), visited Fermyn Woods on May 24th 1942, likely at the emergence peak, and captured 122 *C. palaemon*. The following day, Humphrey collected 33 specimens. Cripps returned to Fermyn in 1943 and collected 55, however there were no 1943 specimens attributed to Humphrey in the Wiltshire collection. On May 24th 1944, Humphrey took 31 *C. palaemon* from Fermyn, and Cripps 26 on May 28th. Between 1947-53, Cripps and Humphrey took a further 21 *C. palaemon* from Fermyn. It is not known whether the men were aware of each other, but collectors of the time were considered very competitive (D. Green, personal communication).

Only 10 more recent Fermyn records were identified, dated between 1956-64. A total of 312 specimens were collected from Fermyn across four flight periods in the early 1940s, however only one specimen – held at the NHM and labelled 'Laundimer' (Laundimer Wood in the Fermyn Woods complex) – was dated 1941 (BMNH(E): 1365098). John Keith Bates' diary describes how he, Don Tozer, and Arthur L. Goodson (then of Tring Museum) collected 120 of 150 *C. palaemon* they saw at Wakerley Woods on May 25th 1947 (Figure 3.5). Bates' accounts were corroborated by the presence of 'A.L. Goodson' and 'D. Tozer' Wakerley Woods specimens from 1947 at the NHM, Glasgow Museums, National Museums Liverpool, and RAMM. However, they collectively numbered only 27 (22.5%) of the 120 *C. palaemon* known to have been taken from Wakerley that year.



one of the narrow rides leading away from the entrance. It was dark green in colour, woodlouse shaped like all Hairstreak + Blue larvae and had a double row of red marks down the back.

5 or 6 Grizzled Skippers feeding on bugle flowers. This species is very fond of bugle.

Remarkable abundance of lepidopterous larvae – winter moth larvae were present in myriads (Due to the fact that the severe winter prevented disease which might occur in a mild one?)

Tuesday May 20th

Saw a ♂ Orange-Tip on the side of the road between Coppice leys + the Spinney.

Wednesday May 21st

Saw another ♂ Orange Tip.

Friday May 23rd

Saw 2 chequered skippers flying together (gambolling flight) over the road between Coppice leys + the Spinney – Courtship?

Sunday May 25th

Sunny and warm. Went with Mr D. Tozer + Mr Goodson of Tring Museum, Herts.

Forestry Commission, Wakerly, Northants: —

About 30 Pearl-bordered Fritillaries. Many were flying up and down a wide grassy path on the side of St Mary's Wood.

Mr Goodson found 1 Green Hairstreak on a grass blade near the gate onto the road (at the oak)

7 or 8 Duke of Burgundy Fritillaries were caught

Saw 8 Dingy Skippers + 10 Grizzled Skippers (Caught 3)

Saw about 150 Chequered Skippers. Mr Goodson caught about 80 for the Tring Museum collections. Mr D. Tozer caught 15 + myself 25.

Monday May 26th

Saw ♀ Chequered Skipper between Coppice leys + the Spinney. Quite a few ♂ Orange-Tips. 2 Holly Blues.

**Figure 3.5**: A page from J.K. Bates' diary held at Leicestershire County Council Museum Collections in Barrow, on which Bates describes seeing 150 *C. palaemon* at Wakerley with A.L. Goodson and D. Tozer on Sunday, May 25th 1947 (Image credit: Leicester Museums).

## 3.4 Discussion

The number of Wakerley records from 1947 suggests the wood's *C. palaemon* population was large by modern standards, but Bates' diary entry does not suggest that the quantity seen or collected was at all surprising or unusual. Other collectors may have seen similar numbers elsewhere in Rockingham Forest that year – as was the case in the early 1940s at Fermyn Woods. That only 22.5% of Bates, Tozer, and Goodson's 1947 Wakerley specimens have been located suggests new data from UK museums, private collections, personal accounts, and other sources represent only a fraction of all uncollated data that exist or ever existed. Monty Tyler's 1972 photograph taken at Addah Wood, for example, is the only evidence that *C. palaemon* colonised the Rutland site (Figure 3.6). The original 35mm slide is held in a private collection and a print was acquired by a Butterfly Conservation County Recorder seeking to improve understanding of butterfly species richness and distribution in Leicestershire (A. Russell, personal communication).

It is possible that a large percentage of uncollated data – especially those in private hands – were lost or destroyed, given biological specimens are fragile and vulnerable to pest damage (Pinniger and Harmon, 1999). Bates' diaries make it clear that he collected extensively, yet his collection at Leicester Museum consists of only six drawers and three *C. palaemon* specimens. Tozer's Coleoptera collection and 1937-70 diaries were also donated to Leicester Museum, but his Lepidoptera collection was sold at auction to a non-entomologist and is now feared lost, as are his 1956-61 diary entries (A. Russell, personal communication). The private Wiltshire collection containing 319 complete *C. palaemon* specimens has been placed in storage since label transcription took place.

There is no evidence that mass collecting took place at Fermyn Woods after 1944 and Wakerley Woods after 1947, despite *C. palaemon* being described as common and fairly plentiful at Wakerley as late as 1957 (Farrell, 1973). While *C. palaemon* populations remained healthy at key sites, it is unlikely collectors would have been motivated to search for other localities where the butterfly was abundant, as "only limited availability would have driven a search for new sites" (S. Clarke, personal communication). However, in 1948 – the year after Bates, Tozer, and Goodson collected 120 *C. palaemon* at Wakerley – Tozer comments in a May 16th diary entry that there are "very few Paniscus about and apparently they are quite scarce, but other butterflies [are] abundant." *C. palaemon* is again described by Tozer as scarce at the site in 1949 (Tozer, *c*. 1937-70). Bates, however, notes "quite a number of chequered skippers – not so many as usual at this time of year [as] in other years" in an entry dated June 5th, 1949 (Bates, *c*. 1945-50).

**Figure 3.6**: Scan of 35mm slide of a ♂ *C. palaemon* photographed at Addah Wood, Rutland in June 1972 (Image credit: Monty Tyler).

A total of 23 *C. palaemon* were caught at Wakerley in 1950 (Farrell, 1973), however none of these specimens have been located during the course of this study. Numbers are only described as fair at Fermyn in 1950 (Farrell, 1973), and only 19 records dated after 1950 originate from the complex, compared to 48 from Wakerley. Textual records from Castor Hanglands (84 from 1961-63), Luffenham Heath (48 from 1968), and "between 30 and 40" from Skellingthorpe (1953) (Farrell, 1973; Duddington and Johnson, 1983) show that healthy colonies were documented where present in the 1950s and 1960s. *C. palaemon* was thought to have been lost from Fermyn by 1961 according to Farrell's report (1973), however two 1964 records have since come to light in the BNM database and a published text (Izzard, 2018). The last Wakerley record remains 1961 (BNM).

This is not to suggest collecting drove *C. palaemon* to local extirpation at Fermyn and Wakerley. Rather, it is an example of a novel, anthropogenic pressure evidenced through museum and private collection data that, when combined with major drivers of decline such as coniferisation and coppice abandonment (Peterken and Harding, 1974; Peterken 1976; Moore, 2004; N. Orchard, personal communication), may have marginally accelerated decline at both sites. Mark-release-recapture (MRR) studies have shown populations to be much higher than casual observations demonstrate (e.g. Thomas, 1983a; Warren, 1983). Collecting is unlikely to drive butterfly species to extirpation unless population size has already become very small due to other pressures. Brereton (1997) determined it was possible to remove up to 50% of a population present on one day by MRR when numbers were low (<50 individuals). However, even with intensive sampling, only 5% of the total population could be removed per day. He concedes, however, that the effect of collecting was likely to be slightly underestimated by MRR. The quantity of museum and private specimen data presented in this study merely demonstrates how plentiful *C. palaemon* once was where found. Scenes of "12 in the net at one time" (as was the case at Legsby and Lynwode Woods in 1890) (Farrell, 1973) are unfathomable in the present day due to shifting baselines of expectation about butterfly abundance (Shirt, 1987; Warren *et al*., 1997; Fox *et al*., 2022).

The large colony present at Luffenham Heath golf course in 1968 according to Macqueen (1969) and Farrell (1973) indicates a minimum nine-year occupation of the Rutland site (1968-76). Compared to existing BNM data, the duration of occupation has now been increased to 45 years (1932-76). Earliest known occupation was initially increased to 32 years (1945-76) after National Museums Liverpool provided a scanned Lancashire and Cheshire Entomological Society collection record card with the wording 'Luffenham Heath G.C., Rutland - (12) - 09.05.1945'. These 12 specimens indicate that the Luffenham Heath area was colonised whilst still continuous heathland known as South Luffenham Heath and Barrowden Leys, "an expanse of heath grassland and scrub, stretching northeastwards from Barrowden towards Ketton […] ploughed over by 1950" (Messenger, 1971). Construction of the golf course began in 1909 and finished in 1911. The 1945 specimens add credibility to 1942-46 Tozer diary entries, which mention a "small wood near Barrowden" at which *C. palaemon* was present "in hundreds" (Tozer, *c*. 1937-70). The small wood was determined to be Coppice Leys, 200m south of the golf course. An entry dated May 23rd 1947 in Bates' diary states that he saw "Two Chequered Skippers flying together (gambolling flight) over the road between Coppice Leys and the Spinney – Courtship?" (Bates, *c*. 1945-50). The spinney in question was Culligalane Spinney.

An image of a 1932 Luffenham Heath specimen labelled with the collector name 'Mason, A.G.L.' was later found on an archived eBay listing (A. Russell, personal communication). Rather than being an isolated site at which *C. palaemon* merely hung on at in its final years, the broad timespan of occupation and quantity of Luffenham Heath records – comparable to key sites in Rockingham Forest – suggest the site may have driven the metapopulation dynamics of its sub-landscape for several decades. Agricultural intensification and insufficient woodland management (Messenger, 1971) is believed to have confined *C. palaemon* to Luffenham Heath by the 1950s. As the earliest known record from the site is dated 1932 – 21 years after construction of the golf course was completed – it is not known whether development of the heathland for recreational purposes had any impact on local abundance.

A general decline in records beginning in the late 1950s is not considered to be an artefact of reduced collecting, as the number of specimens from 1956 (134) exceeds the highest total from any year in the

1920s or 1930s. The introduction of collecting restrictions at East Midlands NNRs from 1964 (Collier, 1986) and growing scarcity of *C. palaemon* at key sites in the 1950-60s is jointly responsible for lower numbers of more recent specimens. Although few conclusions can be drawn regarding the status of *C. palaemon* after the mid-1960s using specimens alone, museum data have lengthened the duration of occupation at key sites compared to existing BNM data, including Luffenham Heath (the last locality in England at which *C. palaemon* was sighted), Wakerley Woods, Castor Hanglands, Bedford Purlieus, and Fineshade Wood.

A large quantity of new data are concentrated around the mid-20th century – the time when the decline of *C. palaemon* in England is believed to have begun (Collier, 1986; Ravenscroft, 1992). Although most records originate from Rockingham Forest, Rutland, and Lincolnshire, records spanning over a century (1827-1935) from the south coast suggest colonies may have been present in Devon, Dorset, Hampshire, and Kent. It is plausible that *C. palaemon* once occupied the Weald, given it featured the largest area of woodland in Medieval England (Rackham, 2000). Several historic texts describe Devon, Hampshire, and Dorset occupation (e.g. Dale, *c*. 1810-1830; Morris, 1853; Westwood, 1854; Newman, 1869), as do nine museum specimens meeting quality control criteria dated 1886-1930. It is possible that south coast colonies were waning even before the advent of butterfly collecting and recording (Barrett, 1893).

*C. palaemon* was anecdotally regarded as very common and "in no danger of extinction" as late as 1961 by Pilcher (1961), and "incomparably more numerous than it was [30 years ago]" at one site in 1957 (Lane and Rothschild, 1957). No effort to systematically evaluate the butterfly's status nationwide occurred until Farrell's 1973 report, after which the extirpation of *C. palaemon* was inevitable. Little mention of a decline in numbers was made prior to 1976, although Pilcher accepts that the species "no longer enjoys its former abundance" at Castor Hanglands in 1961 (Pilcher, 1961). Collier (1966) still considers the butterfly to be common there between 1961-65, however.

## 3.5 Conclusions

A majority of *C. palaemon* records provided by museum collections met quality control criteria for inclusion in this study. Anonymous specimens and those with incomplete label data were in the minority. Many museums are in the process of digitally cataloguing their butterfly collections to ensure specimens are preserved for future generations to access (Figure 3.7). The substantial increase in *C. palaemon* records we have generated has been made possible thanks to the digitisation of museum collections in the 21st century, and better connectivity between researchers and museums thanks to email distribution lists and social media.

Museum data have confirmed the historic range of *C. palaemon* and infilled distribution between 1798-1976 in the species' known Rockingham Forest and Lincolnshire strongholds (Farrell, 1973; Collier, 1986; Ravenscroft, 1995; Moore, 2004), increased record abundance, and lengthened the known duration of occupation at key sites. The large contribution museums have made to this study in the form of both specimens and textual archives has allowed us to draw stronger conclusions about the species' possible rapid extirpation. Timings of anthropogenic and environmental drivers of decline such as clearfelling of medieval broadleaf woodland, coppice abandonment, high forest conversion, conifer afforestation, and agricultural intensification coincide with a decline in records in the mid-1900s. Although predominately based on circumstantial evidence, these drivers are already generally accepted to have played a role in the decline of *C. palaemon* in England (e.g. Farrell, 1973; Lamb, 1974; Peterken and Harding, 1974; Peterken, 1976; Collier, 1978, 1986; Ravenscroft, 1992; Moore, 2004).

This study has focused on documenting the process of collection and collation of new data and presenting initial findings. The enhanced dataset will now be used to look in more detail at the relative significance of factors possibly contributing to extirpation, not just at landscape-scale, but per site. It will lead to improved knowledge of habitat requirements and generate valuable information for potential future butterfly reintroductions in Rockingham Forest, as well as other conservation work such as habitat management. The quantity and quality of uncollated *C. palaemon* data obtained from museum and private collections and texts demonstrates the vast potential of these sources of information for use in studies of other extinct, threatened, or vulnerableUK butterfly species.

Museums should be considered the foremost point of contact for researchers seeking to obtain historic spatiotemporal data for other UK butterfly species that are similarly poorly understood to improve knowledge of their historic distribution, range, and abundance. The methods outlined in this study offer a novel approach to accessing data held by museums and other sources of uncollated data not held in central databases such as the BNM. However, considerable time and energy must be invested in order to build a dataset of records comparable to the one we have built for *C. palaemon* in England, given the number of institutions, individual collaborators, and types of sources that were involved in its creation.

**Figure 3.7**: A digitally photographed *C. palaemon* specimen housed at the University Museum of Zoology, Cambridge. The label reads: ‘Ashton Wold, Northants., W.G.S. 4.VII.1930’ (Image credit: University of Cambridge).

# 4

# Analysing the Decline and Extirpation of the Chequered Skipper Butterfly *Carterocephalus palaemon* in England Using Historic Data

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## Abstract

The chequered skipper butterfly *Carterocephalus palaemon* was declared extinct in England in 1976 after a rapid decline thought to have begun in the 1960s. Here, we use 3,800 historic records collated from museums, published and unpublished texts, and an existing Butterflies for the New Millennium (BNM) database to determine the extent of *C. palaemon*'s former range, abundance, and distribution in England. Geospatial data from formerly occupied sites is used to assess whether landscape permeability, habitat area, site occupation duration, record abundance, and metapopulation dynamics affected colony resilience to local extirpation. We use last record years at sites to create extinction trajectories to assess the butterfly's rate of extirpation in England, and relate breakpoints to environmental and anthropogenic drivers of decline at landscape, sub-landscape, and site level. We explore whether current understanding of *C. palaemo*n decline and extirpation in England is supported by trends in new historic records, and evaluate the apparent connectivity requirements of the species in respect to its ongoing Butterfly Conservation-led reintroduction to the Rockingham Forest landscape. We find that the decline of *C. palaemon* in England did not begin in the 1960s as is currently understood, but around a decade earlier in the late 1940s-early 1950s. We also find that historic colonies at larger sites – and those within metapopulation networks of sites <2km apart – were buffered against local extirpation to a greater extent than colonies at smaller, more isolated sites.

## 4.1 Introduction

Butterfly distribution and abundance has declined in the UK and elsewhere in Europe, with 8% of resident species now extinct and overall numbers declining by around 50% in the UK since 1976 according to the UK Butterfly Monitoring Scheme (UKBMS) Index of Abundance (Pollard, 1977; Dennis *et al*., 2016; Middlebrook *et al*., 2020; Fox *et al*., 2022). UK habitat specialists have shown a steady decline in abundance of 68% since 1976 – the year the UKBMS started (Pollard and Yates, 1993; DEFRA, 2021b). Trends show that butterfly distribution declined in the Netherlands by at least 80% on average between 1890-1940 before monitoring began (van Strien *et al.*, 2019). Pan-European trends for widespread European grassland butterflies indicate a decline of 39% since 1990 (van Swaay *et al*., 2019).

The 2010 Red List for European butterflies shows that 19% of European butterflies are either threatened or declining rapidly, however this likely underestimates the overall threat to European butterflies due to a paucity of data available from eastern Europe (van Swaay *et al*., 2010, 2011). Many UK species that have undergone rage expansion since 1976 (30%) are generalists occurring or breeding in a wide range of habitats, not specialists that have seen their habitats decline in quality and become highly fragmented (Hanksi, 1999; Thomas *et al*., 2001). Fragmentation has been severe in the UK and much of Western Europe and is a major ongoing concern (Hanski, 1999; European Environment Agency, 2011).

A revised Red List of British Butterflies now categorises 28 species as threatened (45%) – an increase on the 23 species listed as threatened in 2010 (Fox *et al.*, 2011, 2022). Four previously native UK butterfly species have been officially declared regionally extinct: the large tortoiseshell *Nymphalis polychloros*, black-veined white *Aporia crataegi*, large copper *Lycaena dispar*, and mazarine blue *Cyaniris semiargus*. However, *N. polychloros* has recently been found at Knepp in West Sussex and Portland in Dorset.

*P. arion* was successfully reintroduced to Devon in 1983 (Thomas *et al*., 2009) and, more recently, *C. palaemon* to England in 2018 as part of a landscape-scale project led by Butterfly Conservation. *C. palaemon* is found in Central and North Asia to Japan, Eastern, Central and Western Europe, and North America, where it is known as the Arctic Skipper (Bink, 1992; Bird *et al*., 1995; Tolman and Lewington, 2008). The species was reported in western Scotland in the 1940s (Mackworth-Praed, 1942), although the first sighting may have been decades earlier (Joicey and Noakes, 1907). *C. palaemon* is excluded from Red List assessment as it has not been established as a resident breeding species in England for five or more years, however it is considered Nationally Scarce according to a rarity assessment (resident in 16-100 10km hectads) (Fox *et al*., 2022). The species is not currently regarded as threatened in

Europe and is categorised as Least Concern on IUCN Europe and EU27 Red Lists (van Swaay *et al*., 2010).

Prior to reintroduction, *C. palaemon* was last recorded in England in 1976 (Archer-Lock, 1982) following a rapid decline believed to have been caused by coniferous afforestation, coppice abandonment, insufficient and inappropriate woodland management, and other environmental and anthropogenic drivers (e.g. Farrell, 1973; Lamb, 1974; Peterken and Harding, 1974; Peterken, 1976; Collier, 1978, 1986; Warren, 1990; Ravenscroft, 1992, 1994a, 1994c; Moore, 2004). *C. palaemon* is known to have occupied damp, sheltered woodland rides and edges, heath grassland, scrubland, fenland, and glades in England, however most museum and private specimens originate from large woodlands in Northamptonshire, Cambridgeshire, Lincolnshire, and Leicestershire (Wildman *et al*., 2022).

It has been suggested that destruction of other marginal habitat such as hedgerows and field margins due to post-war agricultural intensification may have increased colony isolation, thereby limiting gene flow between sites, potentially leading to increased genetic drift (Dempster, 1991; Ravenscroft, 1992). Reestablishment was attempted at Bardney Limewoods in Lincolnshire between 1995-99 using *C. palaemon* collected in northern France and southern Belgium (Warren, 1995a). The project is considered to have failed due to adults being released in poor and unmated condition, the suspect quality of captively-reared eggs, limited availability of high-quality habitat within the woodland complex, and bad weather during both main release years (Moore, 2004).

Research on butterfly species' dependence on spatial distribution of habitat, patch dynamics, and metapopulation biology is well-established (e.g. Levins, 1969, 1970; Harrison, 1993; Hanski and Simberloff, 1997; Hodgson *et al*., 2009; Wood *et al*., 2018). Here, our aim is to identify whether the enhanced dataset of historic records collated in Wildman *et al*. (2022) replicates the currently understood spatiotemporal pattern of decline in England. We use last record years at sites to create extirpation trajectories to assess the butterfly's rate of extirpation in England, and relate breakpoints to environmental and anthropogenic drivers of decline at landscape, sub-landscape, and site level.

New insight into adult *C. palaemon* movement and dispersal, gained since the butterfly's reintroduction to Fineshade Wood in Rockingham Forest, is used to determine to what extent habitat connectivity likely buffered colonies against local extirpation. We use site area and isolation measures, quantity of records, distribution, and range to explore how trends in our enhanced dataset of historic records reflect what was happening in core English landscapes in the 1900s, and infer how metapopulation dynamics may have changed in response to generally accepted drivers of decline. Through this study of historic data, we consider to what extent habitat area, site connectivity, and landscape permeability contribute to both the historic decline and extirpation of *C. palaemon* in England.

## 4.2 Methods

### 4.2.1 Site Analysis

Record data were collated from labels attached to pinned *C. palaemon* museum and privately-owned specimens, published and unpublished texts such as ecological reports and diaries, the BNM database, anecdotal evidence, and butterfly historians. In total, 3,534 new records were added to 266 existing BNM records (for full details of how historic records were obtained for this project, see methods in Wildman *et al.*, 2022). A worksheet containing site and vice county data was created and filtered using strict quality control criteria. The dataset included the names of human settlements, geographically and non-geographically distinct sites, large woodland complexes, vague areas (e.g. Wing railway bank), and range outliers. The initial 135 sites were reduced to 82 using two-or-more records criteria: sites with single records were excluded to ensure hoaxes or misattribution did not influence results. At this stage in filtering, four extirpation trajectory models were generated in R (R Development Core Team, 2005) using last record years for the remaining 82 sites. Afterwards, outlying sites from counties such as Hampshire, Kent, and Devon (Coleman, 1860; Meyrick, 1895; Newman and Leeds, 1913) and human settlements with records attributed to them were excluded from the dataset.

The two-or-more criteria was applied to remove sites with records spanning less than two years. Close-proximity sites (<50m apart, with exceptions) were interpreted as continuous habitat when separated by grassland, scrub, agricultural land, or single linear features and combined to create single sites. Non-geographically distinct sites (e.g. named woodland continuous with other woodland within a larger complex) were treated the same way. A 1947 entry in entomologist John Keith Bates' diary stated that he observed "2 chequered skippers flying together (gambolling flight) over the road between Coppice Leys and the Spinney" near Luffenham Heath in Leicestershire (Bates, *c*. 1945-1950). Coppice Leys and Culligalane Spinney were found to be separated by a road, and *C. palaemon* was known to be present at both sites. A solitary 1971 record from a railway bank near Wing in Leicestershire (northwest of Wakerley Woods and Luffenham Heath) suggested *C. palaemon* may have utilised linear features to traverse landscapes. No evidence was found to indicate such features represented barriers to dispersal for *C. palaemon* in England. Furthermore, a Scottish female *C. palaemon* was seen flying down a stream over 6km from a known site in Scotland in the late 1980s, whilst others were found several kilometres from apparently suitable habitats (Ravenscroft, 1992). Traffic volume was also lower when *C. palaemon* was historically on the wing in England (Havaei-Ahary, 2021).

Records with uncertain provenance such as those attributed to human settlements (e.g. Corby) were excluded from the dataset after extirpation trajectory modelling. It was not possible to assign hundreds of records (e.g. 287 labelled 'Wansford') to known occupied sites due to the number of candidates in proximity to some settlements. Settlements themselves were considered unsuitable for *C. palaemon* based on existing knowledge of its ecology and habitat requirements (e.g. Farrell, 1973; Ravenscroft, 1992, 1994a, 1994c; Ravenscroft and Warren, 1996; Moore, 2004). Settlements were included in extirpation trajectory modelling to accommodate the possibility that collectors used the names as surrogates for presently unknown colonised sites to maintain their secrecy.

A total of 55 historically occupied sites remained in the dataset after all quality control criteria were satisfied (see Appendix One, Table A1.2 for full list of sites). Two-or-more records data (82 sites) were used for extirpation trajectory modelling. Two-or-more years and records data (55 sites) were used to create an additional extirpation trajectory plot in Microsoft Excel (Microsoft Corporation, 2021). On a worksheet, site names were inputted onto rows in column ‘A’ and their corresponding last record into column ‘B’. A filter was added and data in the last record year column inverted (newest record at the top and oldest at the bottom). Each last record year was assigned a number in column ‘C’, beginning with zero for 1977 (the year following the newest record) and ending with 55 for the oldest last site record (1853). These numbers corresponded to the number of sites remaining. Data were plotted on a line graph to create an extirpation trajectory. *C. palaemon* records were also used to create total records and total occupied sites by decade plots, and 1798-1976 distribution maps.

### 4.2.2 Distribution Mapping: Excluding Complete Records

Historic record data were exported to QGIS (QGIS Development Team, 2021) in .csv format for distribution mapping. The FSC Biological Records Tool (Field Studies Council, 2022) was used to import records which were overlaid on a Google satellite map layer. Polygons were drawn around boundaries of occupied sites. National Library of Scotland (National Library of Scotland, 2022) digitised maps were used for reference in cases where boundaries had changed since 1976. Distribution maps were created using a GADM administrative boundary line vector layer (GADM, 2018).

New quadrants shown on distribution maps represented new collated data that met quality control criteria, not records that had already been verified and accepted into the BNM dataset. Isolated records from sites in entirely new areas not accompanied by any supporting evidence were considered highly suspect and excluded (e.g. one 1880 record from Old Manor Wood near Norbury in Derbyshire). Records from Kent – a new area – were considered plausible on the basis of their date range (1898-1906, which coincided with years of records from landscapes in Devon and Hampshire) and the abundance of historic coppiced woodland in the area (see Chapter Three discussion on the Weald). Sassoon (1938) mentioned how *C. palaemon* was seen alongside grizzled skipper *Pyrgus malvae* and dingy skipper *Erynnis tages* at Gedge’s Wood near Brenchley in or before 1897. Other outliers were dismissed as misattributions, clandestine releases, or hoaxes that two-or-more records and years criteria was designed to ignore. A single quadrant in Stowmarket, Suffolk was retained due to repeated mentions in texts (Newman, 1869; Meyrick, 1895; Collier, 1986). By contrast, a single 1975 record from Dorset was dismissed outright given it was the first south coast record for 45 years, some 190km from last records in Northamptonshire and Rutland.

An OpenStreetMap Standard layer was used to create proportional symbols and last record year maps. Lawson *et al*. (2019) suggested special consideration should be given to potential chalk grassland habitat patches within 6km of existing sites for the silver-spotted skipper *Hesperia comma* to create "stepping stones" across the landscape. Further to this, Ravenscroft (1992) described how a single *C. palaemon* was observed 6km from a known site. A 6km buffer zone was created around sites to reflect these statements, and the number of occupied sites within each catchment area was tallied. Area and total occupied sites within 1-6km data were exported to Statistical Project and Service Solutions (SPSS) (IBM Corp, 2021) to establish whether statistically significant (ρ-value) correlation coefficients (*r*-value) existed between site area and/or isolation, total, first, and last records, and duration of occupation (i.e. date range of records) per site.

## 4.2.3 Modelling the 20th Century Decline of *C. palaemon*

Segmented modelling via linear regression has been widely used as a means of inferring nonlinear ecological temporal responses to environmental stressors (e.g. Ollerton *et al.*, 2014; D'Amario, 2019; Tomal and Ciborowski, 2020; Habel *et al.*, 2022). These are quantified by threshold responses known as breakpoints (bp). Bp analysis was performed using the 'segmented' library in R (version 4.1.3) (R Development Core Team, 2005) and same methods described in Ollerton *et al.* (2014). Two-or-more records data (82 sites) were used to generate a 2-bp model, a 3-bp model, and two 4-bp models using linear model lm() and generalised linear model glm() commands. Models were run for one to 10 bps, however nothing higher than 4-bps converged. lm() and glm() commands did not work with variance equally for goodness of fit tests: glm() yielded an Akaike Information Criterion (AIC), not an $R^2$ (coefficient of determination) value like the lm() command. Pseudo-$R^2$ was therefore calculated for glm() using the following formula (Faraway, 2016):

$$1 - \frac{\text{Residual Deviance}}{\text{Null Deviance}}$$

The basic segmented() command produced a single regression line through the dataset and a user-specified number of initial breakpoint seeds $n$. The command then segmented the initial line into $n$+1 regression line segments that met end-to-end at the $n$ bps, and iterated the bp positions to generate the best $R^2$ value for lm() and AIC value for glm(). Each model was run 1000 times with different random initial bp seeds per run to identify the best piecewise-linear model to describe the two-or-more records extirpation trajectory site data (Bai, 1997). All bp results in this chapter used 99% confidence intervals (CIs). The 1-bp extirpation trajectory was created using two-or-more years and records data (55 sites). A vertical red line was used to indicate the bp year on the x-axis. The 1-bp plot was created to explore whether simple processing of data that met quality criteria would generate a similar extirpation trajectory to R models. Extirpation trajectories were produced to determine whether bps indicated by the models coincided with potential real-world environmental or anthropogenic drivers of decline in England.

Bp time periods (e.g. 1885-1946) were time periods to which last record years for sites belonged (e.g. if the last record for a site or locality was 1927, the site was placed in the 1885-1946 time period). Mean geospatial values for sites belonging to each bp time period were tabulated. Data were grouped in this way to identify whether the attributes of sites lost in specific bp time periods were similar. 'Nearest network' was used as a column heading on the table. A network was defined as three or more occupied or unoccupied geographically distinct woodland sites <1km apart and >10ha in size. These measures were chosen based on minimum network size and maximum distances between sites within networks in the Butterfly Conservation Rockingham Forest project landscape and smallest known historically occupied site in England (Barrowden Fox Covert – 10.2ha). The historic boundaries of unoccupied heathland, fenland, scrub, and grassland could not be measured with confidence in many cases, so only woodland sites were included.

In table headings, nearest occupied site was abbreviated to nearest site for formatting purposes. A timeline was created to visualise total duration of occupation (excluding the possibility of colony extirpation and recolonisation in the years between first and last record) for sites in the wider Rockingham Forest landscape. A line graph was produced by combining records per half-decade from sites that belonged to each Rockingham Forest project network plus Luffenham Heath to summarise total records per network in the 1900s. Finally, all site data (not using control quality criteria bar the exclusion of settlements) were used to create figures of total sites with records per decade, and total newly-detected sites with records per 5-year time period. The total sites with records chart did not assume continuous occupation in absence of data, so only sites with evidence of occupation in any given decade were included in bar values.

# 4.3 Results

## 4.3.1 Total Records and Distribution

*C. palaemon* data in England were found to be biased to the 1900s, with only 183 of 3,800 total records (2.2%) dated between 1798 (first record year in England) and 1889 (Figure 4.1). A total of 298 records (7.8%) were dated 1889-99, with the remaining 3,374 (88.8%) from 1900-76. Records increased steadily in the first three decades of the 1900s before peaking in the 1940s with 949 records (25.0% of all English records). Records decreased to 548 in the 1950s (a similar total to the 1930s) and 320 in the 1960s. The 1970-76 period produced 72 records, or an average of 10.3 per year – the lowest annual value since 1890-99 (7.4 records per annum).

Total sites with records per decade in England increased from the mid-1850s onwards (Figure 4.2). An initial peak of 21 sites in 1850-59 was more than doubled by a total of 46 sites in 1900-09 – the largest value for any decade between first and last *C. palaemon* records in England. Interest in butterfly collecting peaked in the late Victorian period (Salmon *et al.*, 2000), which may have led to an increase in the number of sites being visited by casual collectors. The total number of sites with records fell during 1910-19 as interest in the pastime waned and World War I (1914-18) arrived. In the following decade, total sites recovered to 26. A rise to 43 sites between 1950-59 precipitated a decline to 28 in 1960-69 and lastly, 20 sites in 1970-79. Barring sudden peaks in the mid-1800s and at the start of the 1900s, sites with *C. palaemon* records increased gradually per decade from the 1850s to the 1950s. Decline in successive decades was not seen until the 1960-79 time period, however *C. palaemon* was still detected at 20 sites in known landscapes during its shortened extirpation decade.

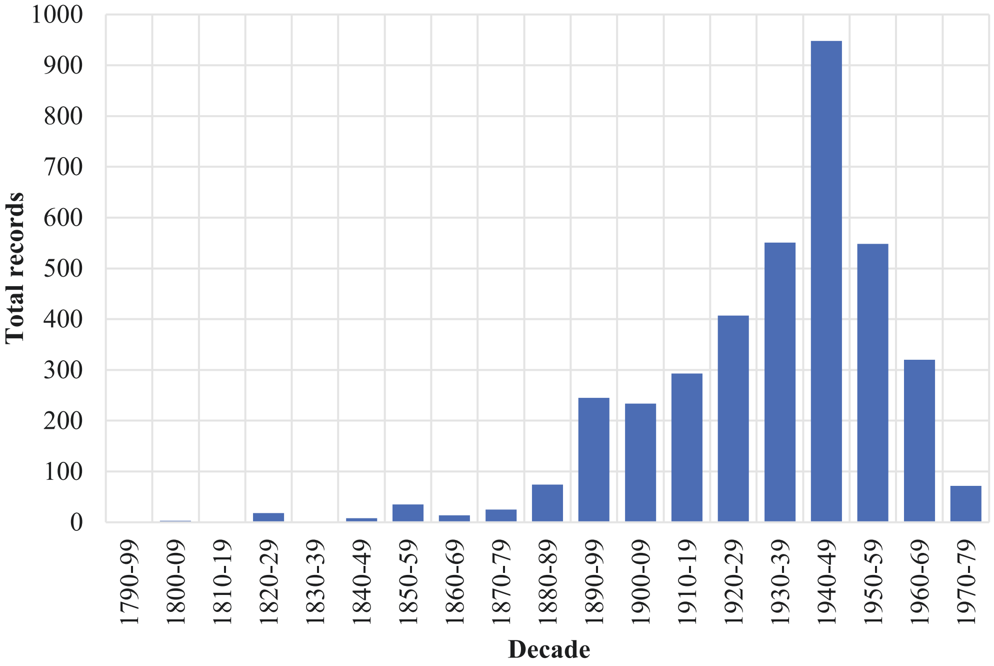

**Figure 4.1**: The total number of *C. palaemon* records by decade in England, 1798-1976. Records increase from the early 1900s and peak in the 1940s before falling sharply in the following decades.

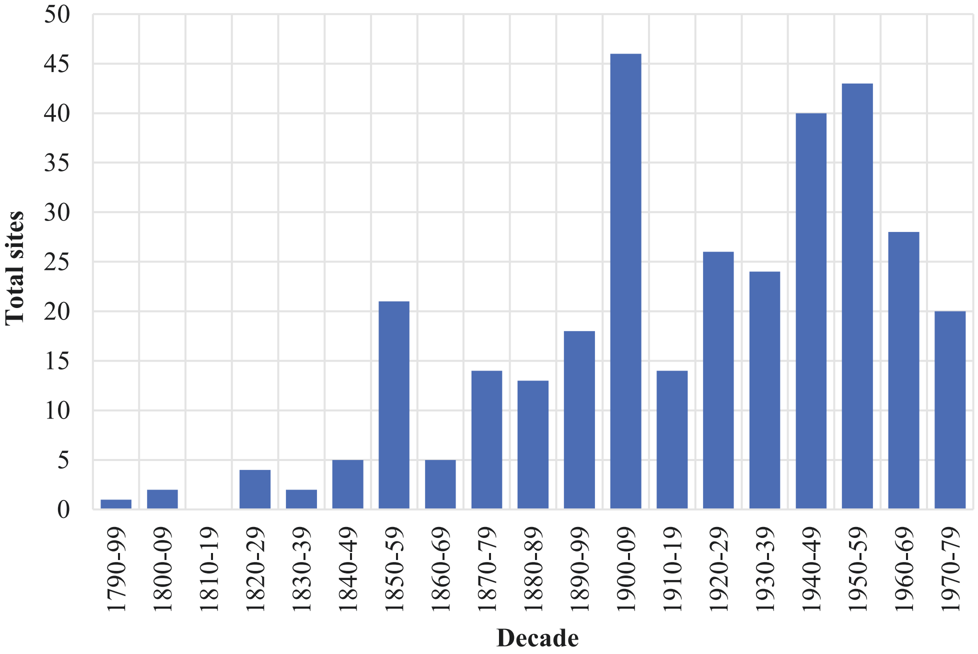

**Figure 4.2**: Total sites with *C. palaemon* records per decade in England, 1798-1976.

New records added Kent (records from 1897-1906) and Dorset (1886-1930) to known *C. palaemon* distribution in England, which increased coverage of the south coast beyond Devon and Hampshire (Figure 4.3). Distribution in established Midlands landscapes was infilled in the decades leading up to extirpation from nine sites in the 1950s, including Bangrave Wood, Southey Wood, Mucklands Wood, and Robert's Field east of Stretton and Greetham Wood on the Rutland-South Lincolnshire border. In the 1960s, two new geographically distinct sites within the same Stretton sub-landscape, Little Haw Wood and Burley Wood (the latter north of Rutland Water) were detected, along with three sites not geographically distinct from sites with earlier records (Cranford Wood and Titchmarsh Wood in Rockingham Forest, and Osgodby Wood in the Willingham Woods complex in North Lincolnshire). In the 1970s, records from Newell Wood (east of Robert's Field), and Addah Wood (conjoined with Little Haw Wood) were also added.

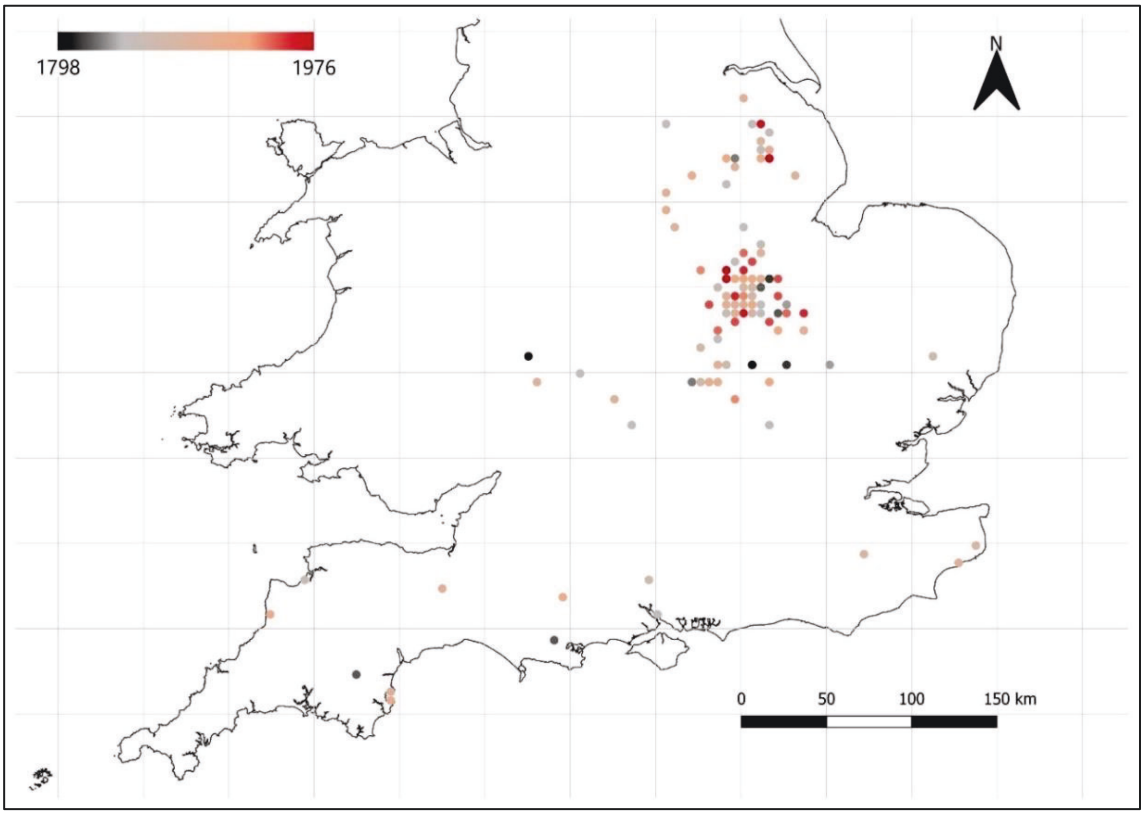

**Figure 4.3**: Quadrants indicating first record year in England, 1798-1976. Note that the most recent quadrants (darkest red) are amongst core landscapes of the Midlands and Lincolnshire, and first years of new areas (Dorset and Kent) are similar to existing quadrants in Devon and Hampshire. The authenticity of spatiotemporal outliers were questioned and kept or deleted accordingly after further investigation using earlier versions of this map. Quadrants added to existing Butterflies for the New Millennium (BNM) distribution data through new records can be seen in Figure 4.4.

Stretton's *C. palaemon* metapopulation may have gone unnoticed for some time after first records from Greetham Wood in 1857. The sub-landscape's next record was from Holywell Wood 86 years later in 1943, and afterwards quickly consolidated, evidenced through first records from the aforementioned Robert's Field (1951), Little Haw Wood (1968), Burley Wood (1969), Newell Wood (1970), and Addah Wood (1972). The rate of detection of sites occupied by *C. palaemon* in the Stretton area outstripped all others in England at the time. Records from a railway bank near Wing, west of Luffenham Heath, and Ring Haw, south of Bedford Purlieus, were the only other new sites in England in the 1970s. New *C. palaemon* records mostly infilled existing BNM distribution between 1798-1976 in the Midlands and Lincolnshire (Figure 4.4), but improved understanding of where the butterfly was present within known landscapes in the years leading up to its extirpation by enhancing existing data at sub-landscape scale.

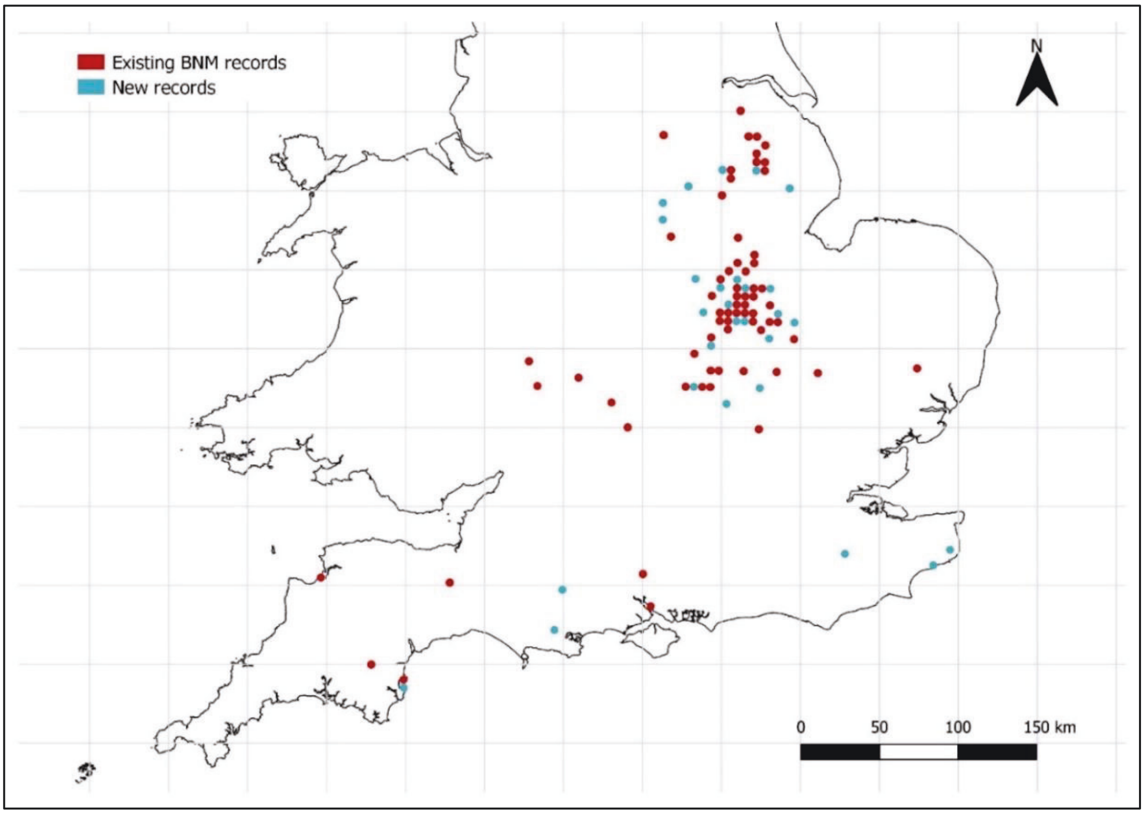

**Figure 4.4**: The distribution of *C. palaemon* Butterflies for the New Millennium (BNM) data and new records in England from 1798-1976 with quadrants to indicate presence, showing infilling of distribution in the Midlands and Lincolnshire.

### 4.3.2 Breakpoint Analysis and Step-Loss

All four extirpation trajectory models using the two-or-more records dataset (82 sites) showed bps in the mid-1940s, ranging from 1946 (rounded to the nearest whole number) for the glm() 3-bp, 4-bpa, and 4-bpb models to 1947 for the glm() 2-bp model (Figure 4.5). Lower CIs ranged from 1945 for the 3-bp model to 1946 for the 2-bp model. Upper CIs ranged from 1946 for the 4-bpa model to 1949 for the 2-bp model. The 3-bp, 4-bpa, and 4-bpb models were more sensitive to the step-loss of sites around 1904. The glm() command found a 3-bp model with bps at both 1905 and 1906. The 4-bpa and 4-bpb models also indicated a bp around 1887, similar to the 2-bp model which suggested a slightly earlier bp of 1885. The 4-bp models were the best statistical description of the dataset ($R^2$=0.9985, AIC=340.74) and were a refinement of the 2-bp model which saw the step-loss of sites in the 1904-06 time period (Table 4.1).

When constrained to two bps, the segmented() command saw 1884-85 and 1947-48 steps. When allowed to fit four bps, the pair of bps around the 1904 step explained more variance than a single bp inserted between 1947-48, replacing the 1884-85 bp and moving the 1947-48 bp back slightly to 1945-46. When allowed to fit four bps, segmented() essentially replicated the 2-bp model, but inserted an additional pair of bps at the 1904 step. The 1945-47 start of *C. palaemon* decline was agreed by all four glm() extirpation trajectory models. However, models were only a baseline that used binary presence-absence site data and assumed continuous occupation of both geographically distinct and non-geographically distinct sites between first and last records (only a single year in some cases). The bp models did not factor in what was happening in the English landscape at the time.

Sites extirpated within the earliest time period of both 2-bp and 3-bp models (1798-1884 and 1798-1904) were more isolated than those lost in later time periods (Table 4.2), however the sample size was much smaller for earlier time periods than later ones (seven sites for 2-bp and 17 sites for 3-bp). The mean distance to nearest occupied site decreased in later time periods in both models. The mean distance to nearest site of 9960.1m for sites lost between 1798-1884 decreased to 1745.6m for those with last record years between 1948-1976 in the 2-bp model, and 9052.4m to 1718.8m in the 3-bp model. Distance to nearest network of three of more sites <1km apart and >10ha in size also decreased between the first bp time period and second time period of both models. Mean distance increased slightly in the 3-bp model from 984.7m (1905-45) to 1163.0m (1946-76) thereafter. The 2-bp model's second time period (1885-1947) captured sites lost up to 20 years earlier than the 3-bp model's second time period (1905-45), further indicating that sites with earlier last records were larger distances from the nearest network of three or more sites. The mean number of occupied sites within both 1km and 2km increased in line with later time periods for both models, suggesting that better connected sites were occupied later than more isolated sites.

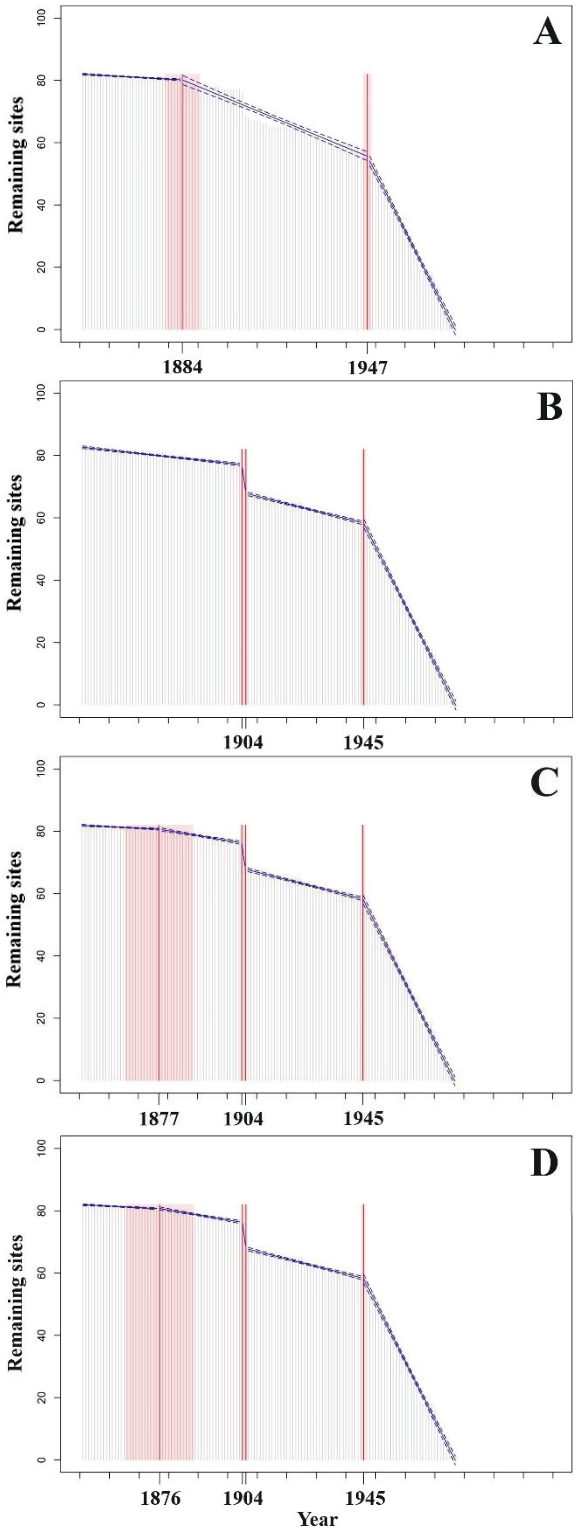

**Figure 4.5**: A) glm() 2-breakpoint (bp), B) 3-bp, C) 4-bpa, and D) 4-bpb extirpation trajectories. Remaining sites are on the y-axis and year is on the x-axis. In the 4-bp model, annual sites remaining are represented as grey vertical columns, line segments as solid blue, and confidence intervals (CIs) in dashed blue (except at 1904 steps on 3-bp, 4-bpa, and 4-bpb models, where insufficient data were available to calculate CIs). Bps are represented as solid red vertical lines and labelled on the x-axis, with CIs as transparent red rectangles around each bp. Missing values in the data were interpolated with values from the previous year.

**Table 4.1**: 2-breakpoint (bp), 3-bp, 4-bpa, and 4-bpb model outputs using glm() commands, showing the lowest Akaike Information Criterion (AIC) value for both 4-bpa and 4-bpb models. Note model agreement for a bp between 1945-47.

| Model | Breakpoint | Lower CI | Upper CI | AIC | p$R^2$ |
|---|---|---|---|---|---|
| glm() 2-bp | 1885<br>1947 | 1879<br>1946 | 1890<br>1949 | 505.71 | 0.9943 |
| glm() 3-bp | 1905<br>1906<br>1946 | 1904<br>1906<br>1945 | 1905<br>1907<br>1947 | 349.93 | 0.9984 |
| glm() 4-bpa | 1877<br>1905<br>1906<br>1946 | 1866<br>1905<br>1906<br>1945 | 1888<br>1905<br>1907<br>1946 | 340.74 | 0.9985 |
| glm() 4-bpb | 1877<br>1905<br>1906<br>1946 | 1866<br>1905<br>1906<br>1945 | 1888<br>1905<br>1907<br>1947 | 340.74 | 0.9985 |

**Table 4.2**: Mean values for historically occupied sites per extirpation time period, as indicated by 2-bp and 3-bp models. Note the inverse relationship between distance to nearest occupied site and number of occupied sites within 1km and 2km per time period.

| Model | Time period | Area (ha) | Nearest site (m) | No. sites within 1km | No. sites within 2km | Nearest network (m) |
|---|---|---|---|---|---|---|
| glm() 2-bp | 1798-1884 | 179.1 | 9,960.1 | 0 | 0 | 10,206.9 |
| | 1885-1947 | 140.0 | 4,642.6 | 0.3 | 0.4 | 1,270.3 |
| | 1948-1976 | 123.9 | 1,745.6 | 1.2 | 1.6 | 1,184.2 |
| glm() 3-bp | 1798-1904 | 137.7 | 9,052.4 | 0 | 0.1 | 5,445.0 |
| | 1905-1945 | 152.4 | 2,018.9 | 0.7 | 0.7 | 984.7 |
| | 1946-1976 | 124.1 | 1,718.8 | 1.2 | 1.6 | 1,163.0 |

A 1798-1976 distribution map created using BNM and new records, which used an average of the last bp value found by each model rounded to the nearest whole number (1946), captured most quadrants in the Rockingham Forest landscape and a majority of those in North Lincolnshire (Figure 4.6). A majority of isolated quadrants elsewhere in England (including all quadrants on the south coast) were mostly captured by the pre-bp 1798-1946 time period.

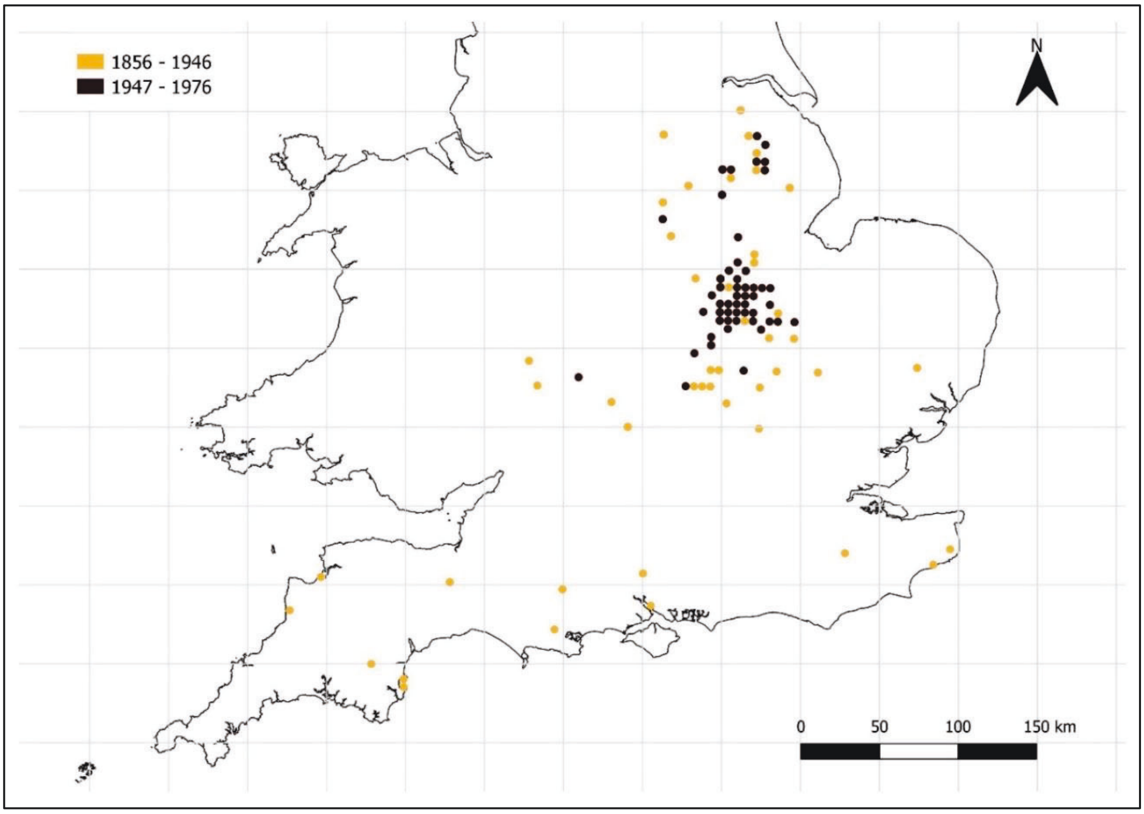

**Figure 4.6**: 1798-1976 English *C. palaemon* last record years in quadrants using 1-bp extirpation trajectory year to illustrate step-loss from the Rockingham Forest landscape after 1946.

### 4.3.3 Wider Rockingham Forest Occupation

All networks officially designated by Butterfly Conservation for the reintroduction of *C. palaemon* to Rockingham Forest (plus the Luffenham network north of Fineshade) were occupied by the butterfly in the 1900s. Fermyn and Fineshade networks saw peak records in 1940-44 and 1945-49 time periods with over 300 records each (Figure 4.7). Four of the six network's peaks exceeded 100 records over a five-year period at least once in the 1900s. Records from Boughton and Southwick remained low throughout the 1900s, only reaching double figures once in the same 1945-49 time period (10 and 14 records, respectively). There were no records from the Boughton network between 1903-47 (a 43-year gap), however if Weekley Hall Wood southwest of Geddington Chase was included in the official network, its single 1905 and 1917 records would have reduced the gap to 30 years.

First records from Bushy Covert and Cranford Wood (also not included in the Boughton network) appeared in 1947 – the same year as Geddington Chase and Old Head Wood contributed all 10 records of Boughton's total for 1945-49. Castor and Barnack's 1930-34 peak (138 records) was the earliest for any network in the wider Rockingham Forest landscape. It was followed by a crash to only seven records in 1940-44. In the figure, note how Castor and Barnack and Fermyn network records trended in opposite directions during this time period. This contrast was mirrored by Fermyn and Fineshade in

1944-49. Castor and Barnack records recovered to 64 between 1950-54 and 97 in 1965-69 after a minor depression before declining to nine in 1970-74. Luffenham Heath's peak was the latest of the featured networks. Although not officially part of the reintroduction project landscape (see Table 4.3), its omission from the plot would have implied that Castor and Barnack was the only network in which *C. palaemon* was still present in reasonable numbers from the early 1960s onwards. Unlike other networks, Fineshade records oscillated in an almost sinusoidal wave between 1900-39, with gradually increasing peaks in records after lulls of equal durations of time. The depression in records during the period of World War II (1939-45) broke the pattern, but was followed by an increase to the network's peak of 306 records between 1945-49 before an equally rapid decline thereafter.

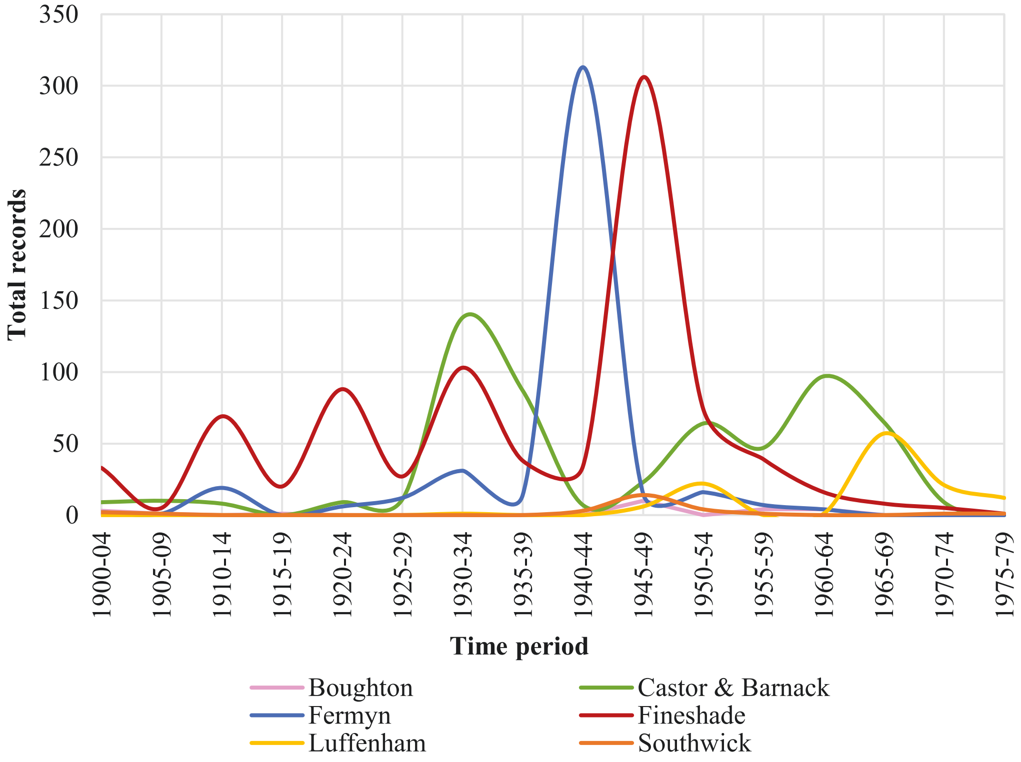

**Figure 4.7**: Total *C. palaemon* records for Rockingham Forest project and Luffenham Heath networks per 5-year period from 1900-76, showing peaks for Castor & Barnack in 1930-34, Fermyn and Fineshade in the 1940s, and Luffenham in 1965-69.

**Table 4.3**: Sites within each official Butterfly Conservation Rockingham Forest project network, plus Luffenham Heath in Rutland.

| Network | Site |
|---|---|
| Boughton | Geddington Chase<br>Grafton Park Wood<br>Old Head Wood |
| Castor and Barnack | Barnack Hills and Holes<br>Castor Hanglands<br>Southey Wood |
| Fermyn | Banhaw Wood<br>Bearshank Wood<br>Blackthorns Wood<br>Fermyn Main Wood<br>Fermyn Woods<br>Laundimer Wood<br>Lilford Wood<br>Oundle Wood<br>Spring Wood<br>Wadenhoe Great Wood<br>Wadenhoe Little Wood |
| Fineshade | Bedford Purlieus<br>Calcining Banks<br>Collyweston Great Wood and Eastern Hornstocks<br>Fineshade Wood<br>Old Sulehay<br>Ring Haw<br>Wakerley Woods |
| Luffenham Heath | Coppice Leys<br>Culligalane Spinney<br>Luffenham Heath<br>Shire Oaks and Welland Spinney |
| Southwick | Cadge and Hostage Wood<br>Dodhaws Wood<br>Glapthorn Cow Pasture<br>Short Wood<br>Southwick Wood (Wildlife Trust BCN)<br>Southwick Wood (Forestry England)<br>Tomlin Wood |

The 10 historically most populous sites for *C. palaemon* records in the 1900s were (in descending order from highest to lowest ): Castor Hanglands, Fermyn Woods, Wakerley Woods, Skellingthorpe Woods, Fineshade Wood, Bedford Purlieus, Luffenham Heath, Barnwell Wold, Monks Wood, and Ashton Wold (Figure 4.8). The 247 records attributed to Wansford in the 1900s could have originated from any site(s) within several kilometres of the village, such as (but not limited to) Castor Hanglands, Bedford Purlieus, Old Sulehay, Ring Haw, and Collyweston Great Wood and Eastern Hornstocks. Dissemination of Wansford records would have had a sizeable impact on total records at one or more of these site(s). The figure should, therefore, only be used as an indication of possible peak years for sites near Wansford, particularly in the 1910s and 1920s (78 and 111 Wansford records, respectively).

The number of records from Wakerley Woods and Fermyn Woods (including Harry's Park Wood and Laundimer Woods) increased in the 1940s to over 300 records each. The tail on Wakerley records was longer than that of Fermyn's, as records from the latter site declined to 23 in the 1950s compared to

Wakerley's 71 from the same time period. However, in the 1960s, records from both sites fell to single figures. Unlike the single peaks of Wakerley and Fermyn, Castor Hanglands peaked twice: once in the 1930s with its highest total for any decade in the 1900s (225 records), and once in the 1960s (160 records) – the highest for any site in this time period.

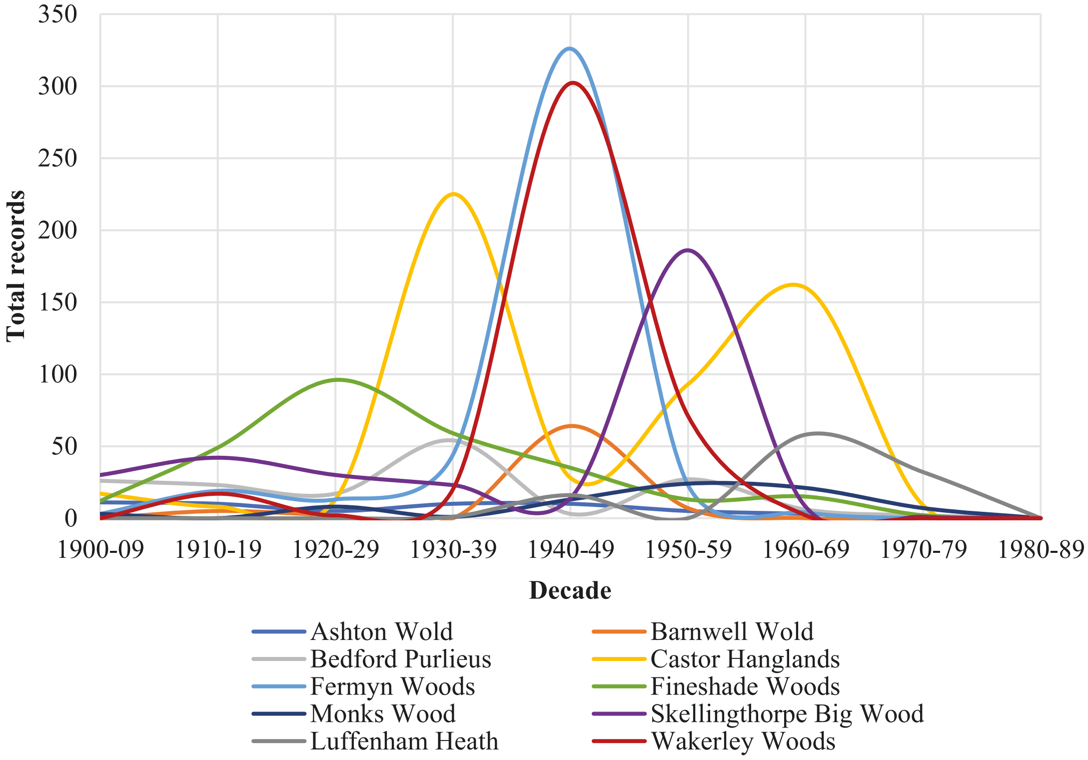

**Figure 4.8**: Total *C. palaemon* records per decade for the top 10 most abundant sites in England between 1900-76. Wakerley, Fermyn Woods, and Barnwell Wold records peak in the 1940s, flanked by Castor Hanglands and Bedford Purlieus (1930s) and Skellingthorpe Big Wood (1950s). These are, in turn, sandwiched by peaks for Fineshade Wood (1920s), Luffenham Heath, and Castor Hanglands once again (1960s).

Luffenham Heath's most abundant decade for records was 1960-69 – the latest peak of all featured sites – and had the most records in 1970-79 (32 records compared to Castor Hanglands' nine). Fineshade Wood's peak (1920-29, 96 records) was lower than other featured sites in the Rockingham Forest landscape, however the trajectory of its subsequent decline was more gradual. Records from Skellingthorpe Woods remained low throughout the early 1900s and declined slightly per decade after 1910-19 until a sudden peak in 1950-59 (186 records). Barnwell Wold's 1940s peak (64 records) mirrored Wakerley and Fermyn, but the site reported less than ten records for three time periods in the 1900s and none for the remaining five. Total records for Castor Hanglands (677) ranked it first in the expanded Rockingham Forest landscape and England overall (Figure 4.9). This was unsurprising given the site was long-regarded as the species' headquarters and known to butterfly collectors as early as 1823 (Salmon *et al*., 1823). Castor Hanglands dwarfed other sites within its network (Barnack Hills and Holes, Mucklands Wood, Simon's and Oxey Wood, and Southey Wood – 30 records combined). Total records were proportionally weighed to northern Rockingham Forest networks of Castor, Fineshade, and Luffenham with a combined total of 1,689. Records from southern networks – Boughton Fermyn, and Southwick – summed to only 492 by comparison, excluding totals from Ashton Wold (57), Barnwell Wold (78), and Oakley Purlieus (28) near Corby.

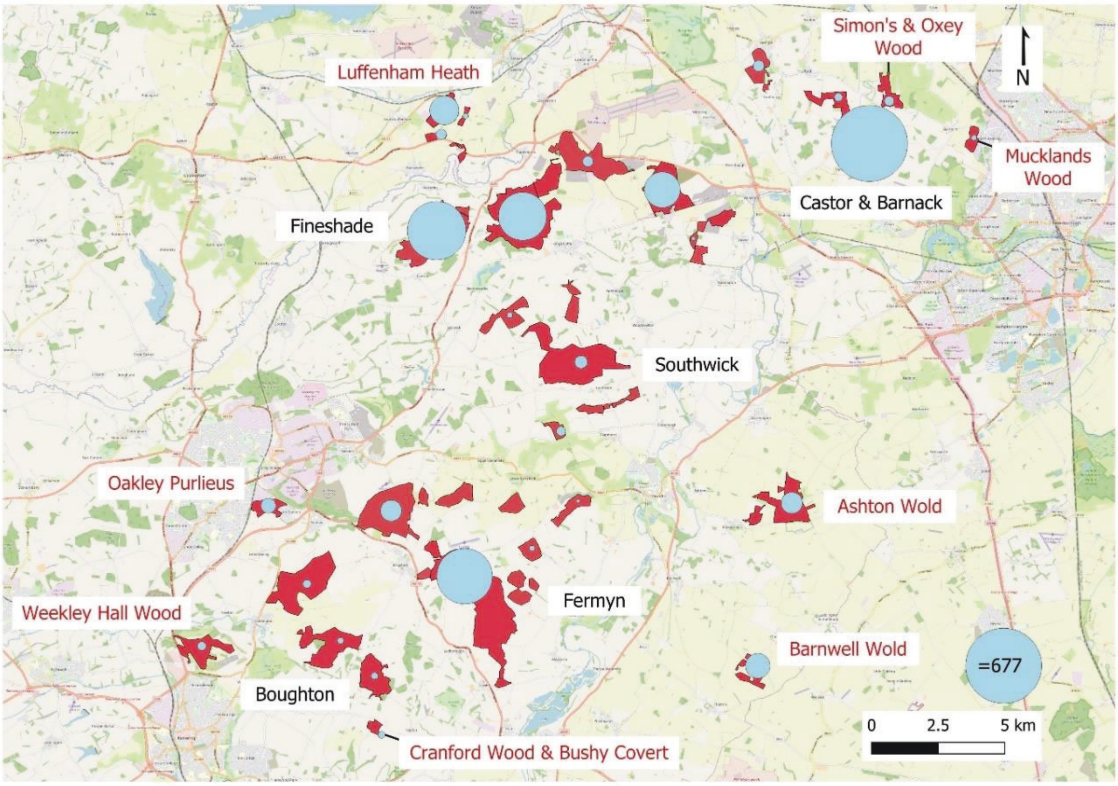

**Figure 4.9**: Proportional representation of total historic *C. palaemon* records per site to illustrate site significance in the wider Rockingham Forest landscape (official Butterfly Conservation networks in black font, unofficial sites and networks in red font). The size of the largest symbol (Castor Hanglands in the northeast) is equivalent to 677 records.

Laundimer and Harry's Park Wood records (56) were able to be distinguished from Fermyn Main Wood records due to specimen labelling conventions, however Fermyn Lady Wood records were not able to be separated in the same way: the historic nomenclature of 'Farming Woods' was assumed to have related to specimens caught at both Main and Lady Wood. A single proportional marker was therefore chosen to represent both sites. Data from the non-geographically distinct Titchmarsh Wood and (historically) non-distinct Lilford Wood were also represented by the same marker. Smaller markers for sites within both Boughton and Southwick indicated a proportionally lower number of records from both networks between 1798-1976 compared to other sites in the landscape. Note their size in comparison to markers from Bedford Purlieus, Fineshade Wood, and Wakerley Woods in the Fineshade network (862 combined records) and the more isolated Ashton Wold and Barnwell Wold to the east of the River Nene.

The last record year for all sites with records within the wider Rockingham Forest landscape was 1947 or later (Figure 4.10). Three sites were dated 1947 (Bearshank Wood, Old Head Wood, and Oundle Wood) and one was dated 1949 (Coppice Leys and Culligalane Spinney). Eight sites were lost in the 1950s, another eight in the 1960s, and seven in the 1970s (Ashton Wold, Bedford Purlieus, Castor Hanglands, Fineshade Wood, Glapthorn Cow Pastures, Luffenham Heath, and Wakerley Woods). From north to the south in the landscape, the Castor network remained occupied until 1974, Luffenham until 1976, Fineshade until 1974, Southwick until 1975, and both Fermyn and Boughton until 1964. Wakerley Woods was the only site in the Fineshade network with a last record date earlier than 1971 (1961). No sites were known to have been occupied in the more southerly Fermyn network later than 1964.

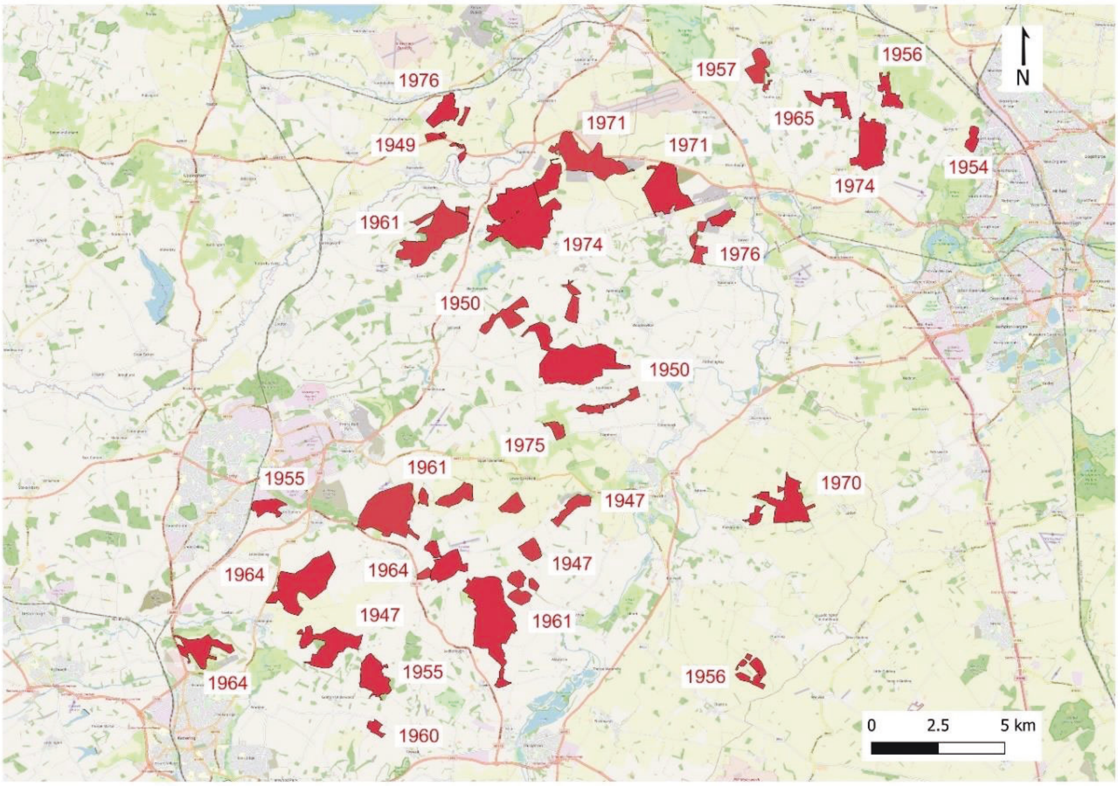

**Figure 4.10**: Last record years for *C. palaemon* at sites with historic data in the wider Rockingham Forest landscape. Note how the latest record for sites south of Corby bar Ashton Wold (1970) is 1964.

Castor Hanglands' 1974 last record indicated a 151-year occupation of the site by *C. palaemon* (1823-1974) (Figure 4.11), equal to Clapham Park Woods (1798-1949) where the butterfly was first recorded in England. Continuous occupation was assumed in the absence of records from every year between first and last record at every site. Other sites not represented on the timeline with notable occupation durations included Bourne Wood (89 years), Greetham Wood (115 years), Legsby and Willingham Woods (106 years), Newball Wood (117 years), Ropsley Rise Wood (114 years), Skellingthorpe Woods (127 years), Stapleford Woods (103 years), Sywell Wood (111 years), and Wardley Wood (92 years). Although Weekley Hall Wood near Kettering was not officially part of the Boughton network, its occupation duration of 107 years was 45 years longer than Geddington Chase (62 years) directly to its northeast, which shared its last record year of 1964.

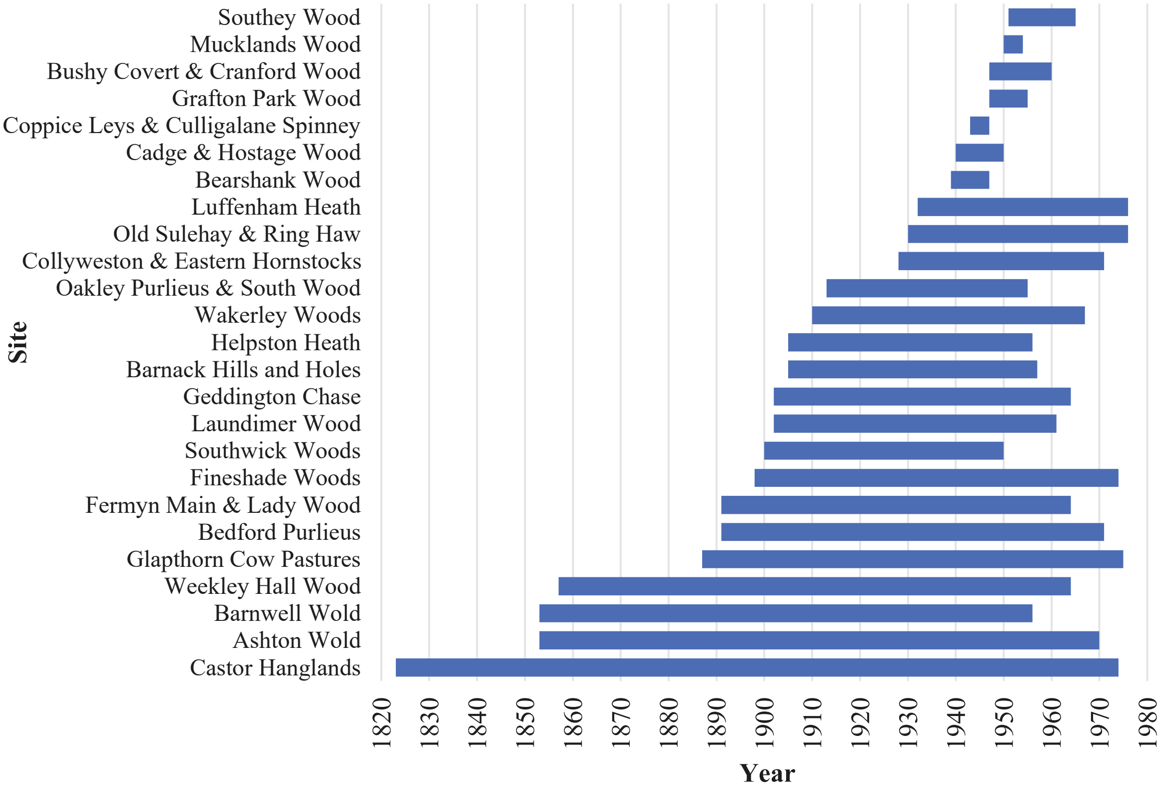

**Figure 4.11**: Timeline of *C. palaemon* site occupation duration in the expanded Rockingham Forest landscape. Castor Hanglands had the longest duration in England overall at 151 years (1823-1974).

Despite the apparent isolation of Barnwell Wold and Ashton Wold east of the A605, both sites were thought to have been continuously occupied by *C. palaemon* for 103 and 117 years respectively, ranking them 11th and joint-ninth out of 55 sites in England overall. Only Castor Hanglands saw a longer duration between first and last record than Ashton Wold. Within the official Rockingham Forest project networks, Glapthorn Cow Pastures (88 years) and Fineshade Wood (83 years) followed Castor Hanglands as the next-longest known occupied sites. Southey Wood was the last site to be detected in 1951, and its last record followed fourteen years later in 1965. Old Head Wood was not included in the timeline, as its first and last records were both dated 1947.

Sites meeting full two-or-more years and records quality control criteria provided a clear signal of when decline began in England – between 1946-47 – in line with provisional breakpoints seen by glm() extirpation trajectory models (Figure 4.12). Site extirpation occurred gradually between 1853 and 1927, during which time four sites were lost. One site was lost four years later in 1929. The close proximity of these last records was responsible for the minor step loss from 51 to 50 remaining sites between 1925-29. No further sites were lost until 1942 (one site) and then 1946, after which point sites were lost annually in a precipitous decline that stalled slightly between 1965-68, when only one site was lost. The steep gradient continued thereafter until last records from the final two known occupied English sites, Luffenham Heath and Ring Haw, in 1976. Extirpation followed in 1977 (zero sites).

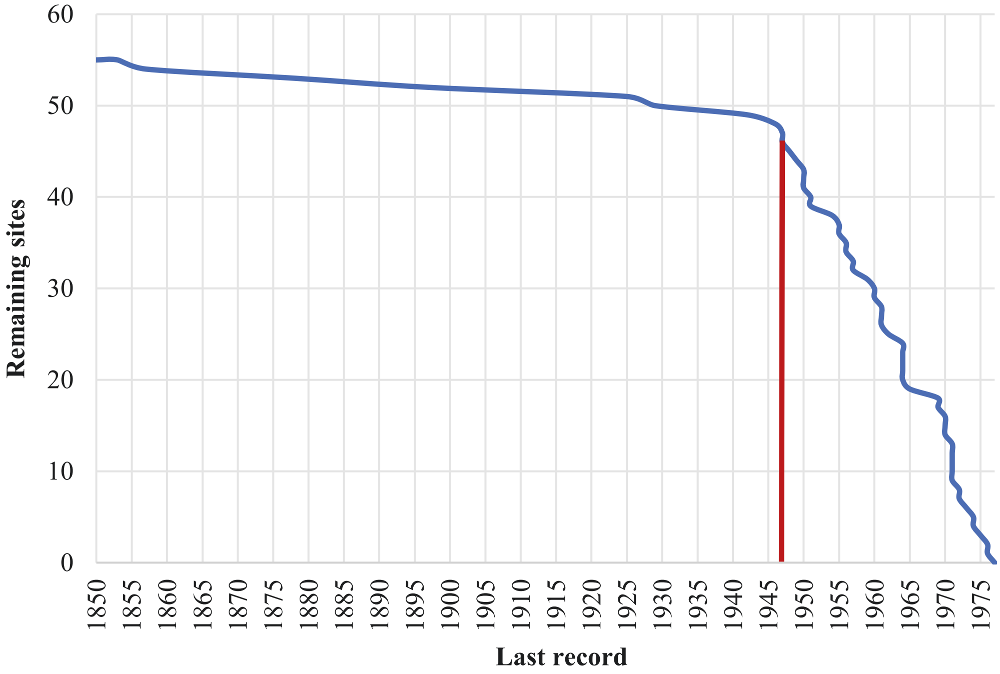

**Figure 4.12**: 1-bp extirpation trajectory using two-or-more years and records (55 sites) data, showing 1946-47 step-loss of *C. palaemon* sites in England and precipitous decline thereafter.

## 4.3.4 Tests of Association

Out of a total 24 tests of association between site area and isolation variables using Spearman correlation in SPSS (IBM Corp., 2021), 15 were statistically significant. Despite significant ρ-values, only weak positive coefficients (*r*-values, indicating the strength of correlations) were found between site area and total records, last record year, and occupation duration (*r*=0.331, ρ=0.013; *r*=0.336, ρ=0.012; and *r*=0.297, ρ=0.028, respectively). Total records were weakly correlated with site area (*r*=0.331, ρ=0.013) and last record year (*r*=0.308, ρ=0.022), moderately correlated with duration of occupation (*r*=0.596, ρ=<0.001), and weakly correlated with number of sites within 1km (*r*=0.298, ρ=0.027). Last record year was weakly correlated with area (*r*=0.336, ρ=0.012), total records (*r*=0.308, ρ=0.022), occupation duration (*r*=0.358, ρ=0.007), and number of sites within 1km (*r*=0.331, ρ=0.013) and 2km (*r*=0.305, ρ=0.023). A positive relationship between occupation duration and total records was expected (the longer a site is occupied, the more records it generated). This was also true for site area and total records (the larger the habitat, the more records it generated) and occupation duration and last record year (the longer a site was occupied, the later its last record in respect to *C. palaemon* extirpation). However, significant coefficients between area and last record year (*r*=0.336, ρ=0.012), total records per site and number of sites within 1km (*r*=0.298, ρ=0.027), and last record year with both number of sites within 1km (*r*=0.331, ρ=0.013) and 2km (*r*=0.305, ρ=0.023) suggested landscape permeability and connectivity, and independently, site area, influenced the resilience of *C. palaemon* populations in historic English landscapes. No statistically significant *r*-values were found in tests between records, duration, and number of sites within 3-6km, however a 3km column was included in the table of results to indicate the distance at which they ceased to be statistically significant.

## 4.4 Discussion

### 4.4.1 Pattern of Decline in England

The decline of *C. palaemon* in England is previously understood to have begun in the 1960s (e.g. Farrell, 1973; Ravenscroft, 1992). Given coppicing declined sharply between the late 1940s-1960s and only 0.1-1% of woodland in the Midlands was actively coppiced by 1965 (Peterken, 1981; Fuller and Warren, 1993), links between coppice abandonment, coniferisation in the 1920-1950s, and the butterfly's decline have been disregarded (Ravenscroft, 1992). However, using breakpoint analysis we have shown that sites were lost precipitously in England from the late 1940s onwards. Habel *et al.* (2022) use breakpoints to study the decline of 168 butterfly and burnet moth species in central Europe over the last century, and find that time windows coincide with periods characterised by habitat destruction and deterioration due to agricultural intensification and land use changes. In Rockingham Forest, urbanisation, mineral extraction through quarrying, and agricultural subsidies (Peterken and Harding, 1974; Peterken, 1976) led to over 400ha of woodland loss during the 1946-72 period, which was balanced by non-equivalent woodland creation of mixed and conifer plantation.

Heavy post-war afforestation and lack of active management such as coppicing and selective thinning – indicated by the even-age of many Rockingham Forest woods – was perhaps linked to a local decline in demand for coppice products from iron and steel works (Heath *et al*., 1984; Orchard, 2007). In 1947, 21.0% of broadleaved resource was classified as coppice in Britain, which declined to 5.2% by 1982 (although total broadleaved woodland increased by 10.8% during this time period) (Hopkins and Kirby, 2007). Rockingham Forest colonies persisted for longer durations of time and deeper into the 20th century in the wake of declining woodland management because enough good quality habitat remained at large sites. Coniferisation of Westhay Wood at Fineshade Wood by 1946 (90.7ha) would have shaded over a proportion of woodland rides, however 41.7ha of coppice with standards and 14.1ha was still cut-over (Orchard, 2007). Deteriorating habitat at Ashton Wold in the 1950s forced *C. palaemon* out of the wood into an area of gorse *Ulex europaeus* and roughs near Polebrook lake (Izzard, 2018), however isolated colonies landlocked by arable farmland were not afforded the same luxury.

Smaller sites were more vulnerable to structural changes. Barrowden Fox Covert, an ash *Fraxinus excelsior* wood as described by Lamb (1974), was felled and replanted with larch *Larix decidua* starting in 1967. Nearby Barrowden Leys heathland was entirely ploughed up by 1950 (Messenger, 1971), likely contributing to loss of *C. palaemon* from neighbouring Coppice Leys and Culligalane Spinney (last record 1949). Later extirpation at open heathland, fenland, and grassland sites such as Luffenham Heath and Woodwalton Fen may have been caused by post-myxomatosis succession due to relaxation of grazing pressure, which eventually crowded out *C. palaemon* larval hostplants such as heath false brome *Brachypodium pinnatum* (Thomas, 1983a; Thomas *et al*., 1986; Ravenscroft, 1990). Nevertheless, good connectivity within the Luffenham network (<1km between sites) enabled its sub-population to persist in the wake of several drivers of decline. Large numbers of 1947 records (e.g. from Barnwell Wold, Fineshade Wood, and Wakerley Woods) follow the winter of 1946-47, indicating colonies at key sites were not negatively impacted by severe spells of weather. Similarly, only one English site is lost between 1965-68 after the 'big freeze' of 1962-63. Good emergence at Fineshade Wood in 2019 after a summer drought in 2018 suggests that even small historic *C. palaemon* colonies were unlikely to have been overly pressured by isolated extreme weather events such as hailstorms (Farrell, 1973).

No records are known to exist from the former heathland of Sutton Heath and Old Sulehay north of Wansford between Bedford Purlieus and Castor Hanglands, and smaller, more obscure patches such as Sutton Wood, however *C. palaemon* may have formerly occupied these sites and used them as connective patches. The existing weak *r*-value correlation between known occupied sites <2km apart and last record year suggests extirpation buffering scaled according to patch occupancy, habitat availability, and sub-landscape site connectivity. This positive relationship would be amplified by new records from unrecorded fringe habitats in close proximity to known occupied sites. The absence of direct evidence of occupation should not be taken as a conclusive sign *C. palaemon* was not present. Given that research into the historic distribution and abundance of any extinct butterfly is likely to feature a degree of speculation to compensate for voids in data, we suggest that fringe habitats such as deciduous woodland, heathland, fenland, and herb-rich grassland may have been utilised by *C. palaemon* to disperse across landscapes prior to the species' decline.

### 4.4.2 Quirks of Quantitative Data

As we will discuss in more detail later in this Discussion, the dataset we have created for this project likely underestimates the true number of historic colonies that existed in England, as it principally uses labels attached to pinned specimens. Many specimens likely remain unaccounted for despite support from museums and private collectors, or have been lost or destroyed in the intervening decades (see Wildman *et al*., 2022). Collectors biased sites where *C. palaemon* was known to be most abundant, and would rarely venture elsewhere in search of the butterfly (e.g. Tozer, *c*. 1937-70; Bates, *c*. 1945-50). Their objectives were quite different to those of 1970s researchers belatedly determining the status of the butterfly in England (e.g. Farrell, 1973; Lamb, 1974; Stark, 1974).

From 1964, a permit system allowed only two specimens to be collected from Castor Hanglands per permit-holder. However, Collier (1986) states there was no evidence collecting had any effect on population size. Over-collecting has been suggested as a driver of butterfly decline in Japan (Nakamura, 2011), but its impact is considered to be minor and geographically confined (Sánchez-Bayo and Wyckhus, 2019). As discussed in Chapter Three, waning abundance at once-populous sites may have driven collectors, butterfly recorders, and enthusiasts to search elsewhere for *C. palaemon* (Pilcher (1961) warns that the butterfly "no longer enjoys its former abundance" at Castor Hanglands). Somewhat paradoxically, landscape consolidation and higher numbers of sites with records in the decades leading up to extirpation may have been indicative of wider decline of the species (see Figure 4.2).

### 4.4.3 Changes in Landscape Permeability

Ravenscroft (1992) suggests that, if English *C. palaemon* expressed traits similar to the Scottish butterfly, it would have required patches of suitable habitat situated between major sites to disperse across landscapes. He notes that Scottish adults were frequently found in patches of flowers by streams and roads between 1988-90. The loss of 36% of hedgerows in England between 1947-85 (upwards of 5000km per year between 1946-63) (Hooper, 1974, 1978; Pollard *et al*., 1974; Countryside Commission, 1989) coincides with 1946-47 *C. palaemon* extirpation trajectory step-loss and pattern of decline thereafter. Agricultural intensification may have been more detrimental to colonies at isolated sites given their greater reliance on movement corridors than those situated in cosier networks. Genetic drift (the change in frequency of genotypes) between *C. palaemon* populations may have increased in line with diminishing habitat suitability and landscape permeability in postwar England. Isolation and colony size contraction may have led to a gradual reduction in gene flow and genetic diversity as inbreeding increased homozygosity and the frequency of deleterious recessive alleles, resulting in a loss of fitness through inbreeding depression. Alleles in larger, better-connected populations would have been present in different frequencies, and their colonies experienced lower genetic drift and higher gene flow than those at more isolated, smaller sites with lower carrying capacity, buffering them against fixation for longer (e.g. Ralls *et al.*, 2013; Star and Spencer, 2013; Szpiech *et al.*, 2013; Mackintosh *et al*., 2019; Gompert *et al*., 2021).

The rapid post-war uptake of herbicides and insecticides such as 2-methyl-4-chlorophenoxyacetic acid (MCPA), 2,4-dichlorophenoxyacetic acid (2,4-D), and 4,6-dinitro-o-cresol (DNOC) in agricultural settings (Handley, 2019a) may have led to spray drift contaminating remaining field and woodland margins. Application became more widespread and grew in popularity from the 1960s onwards (Lockhart *et al*., 1990). Rides were sprayed at Castor Hanglands after clearfelling took place (J. Robinson, personal communication), however it isunclear whether this was with an insecticide such as fenitrothion to combat the pine beauty moth *Panolis flammea* (Holden and Bevan, 1981) or a targeted solution to prevent stump regrowth. The toxicity of herbicides and insecticides known to have been used in arable farmland, forestry settings, and on Luffenham Heath golf course has not been fully explored (e.g. Brown, 1975; Evans, 1983; Davis *et al*., 1991a, 1991b; Çilgi and Jepson, 1995; Kjær *et al*., 2014; Braak *et al.*, 2018).

Record numbers, site area, and last record year at Fineshade Wood, Bedford Purlieus (likely including Collyweston, despite record scarcity), and Wakerley Woods suggests colonies across the Fineshade network were large and that good quality habitat was abundant prior to the late 1940s. The linear arrangement of woodland within the sub-landscape may have benefitted Fineshade Wood the most given its position between Wakerley Woods and Bedford Purlieus, as it would have captured mobile *C. palaemon* dispersing in a both westerly and easterly directions. Varying numbers of records per site and network could have been due to natural population fluctuations and climatological factors (Farrell, 1973; Brakefield, 1991) which preceded a precipitous decline signalled by many key Northamptonshire sites after the 1940s. Later record peaks at Castor Hanglands, Monks Wood (where *C. palaemon* was reported as common until 1959 (Farrell, 1973), and Skellingthorpe Wood suggest that the pressures of deciduous clearfelling and succession, conifer afforestation, timber extraction, and unsuitable management at large, isolated woodland sites were felt at different times across England.

## 4.4.4 Habitat Degradation

The "biological islands" created in the 1900s through loss of marginal habitats due to anthropogenic factors such agricultural intensification, and excessive mowing and ride narrowing at sites such as Monks Wood, Woodwalton Fen, and Castor Hanglands may have accelerated decline at these and other NNRs (Collier, 1978, 1986; P. Kirby, personal communication). Ride management regimes implemented in the 1960s and 1970s were seemingly dwarfed by the scale of commercial forestry operations and had little measurable positive impact on colony size. However, inappropriate practices such as 'auto-scything' are thought to have led to a loss of floristic diversity at Castor Hanglands and Ailsworth Heath by June 1973 and adversely affected *C. palaemon* larvae (Collier, 1966; Farrell, 1973). Ray Collier (Castor Hanglands NNR Warden in the 1960s) is believed to have said the site "wasn't right" for *C. palaemon* despite efforts to improve habitat in the 1960s (J. Robinson, personal communication). In 1937, labour shortages at Fineshade Wood led to maintenance arrears and the acceptance of coppice regrowth in lieu of planted ash *Fraxinus excelsior* and poplar *Populus* spp.. European larch *Larix decidua* and *F. excelsior* plantations also "suffered severely" from regrowth (Forestry Commission, 1952). During World War II, labour supply was further depleted, which led to the rank growth of vegetation. In the years leading up to 1952, an acute labour shortage was still in evidence at Fineshade and Fermyn Woods, which prevented any planting from taking place.

Metapopulation dynamics of *C. palaemon* may have been influenced by landscape permeability, with colonies remaining closed, intermediate, or open depending on habitat area and isolation extent. Ravenscroft (1992) suggests that both adults and larvae may need a large area to maintain a population because *C. palaemon* occurs at such low densities. The relationship between site area, duration of occupation, and last record year found at historic English sites supports this theory. Gene flow within metapopulation networks may have increased mating potential with mobile individuals transiting core habitat where abundance was highest (e.g. Amarasekare, 1998; Kuussaari *et al*., 1998; Bonsall *et al*., 2014).

## 4.4.5 Habitat Fragmentation

Due to significant positive coefficients reported from tests between total records and number of occupied sites within 1km, and date range of records, last record, and number of occupied sites within both 1km and 2km, historic populations of *C. palaemon* appear to have exhibited local variance in mobility. Networks of occupied sites supported healthy colonies able to form intermediate sub-populations that were buffered against extirpation to a greater extent than closed populations at isolated sites. Permeability of sub-landscapes in already healthy networks such as Fermyn and Fineshade and dispersal from Castor Hanglands was likely facilitated by open habitats on surrounding farmland and other suitable patches up to the mid-1900s. Agricultural intensification subsequently destroyed a majority of wetland and unimproved grassland sites, leaving only "fragments" (Collier, 1986). Remaining patches of various sizes may have become more important as a result (Topp and Loos, 2019).

Mineral extraction through quarrying, commercial conifer afforestation, and land use conversion would have inhibited gene flow by increasing fragmentation. Loss of linear habitats such as field margins and roadside verges utilised by Scottish *C. palaemon* (Thomson, 1980; Collier, 1984) may have further limited movements. The significant ρ-value but weak *r*-value between total records and number of sites within 1km ($r$=0.298, ρ=0.027) indicates historic colonies were possibly reinforced by individuals dispersing from nearby sites (Table 4.4). *C. palaemon* has been known to fly as far as 1.7km since its reintroduction to Fineshade Wood in 2018 (see Chapter Five). Out of 30 recaptured individuals, three (10.0%) dispersed >1km from initial capture location between 2019-21, and a total distance of >1km was covered by five individuals (16.7%). This suggests historic *C. palaemon* were able to reach sites 1-2km away. A majority of new sites recorded throughout the history of *C. palaemon* in England are not believed to have been caused by colonisation, however. Detection was likely a result of consolidation of the landscape surrounding a known population, or following the discovery of a colony in a new landscape. The formation of many entomological societies in the 1800s and growing popularity of butterfly collecting as a pastime in the late Victorian period would have led to better understanding of distribution once bias to sites such as Castor Hanglands was overcome (Stephens, 1828; Dale, 1890; Salmon *et al*., 2000).

**Table 4.4**: Two-or-more years and records (55 sites) Spearman correlation coefficients for historic *C. palaemon* site area and isolation variables and number of sites within set distances (***ρ=<0.001, **ρ=<0.01, *ρ=<0.05).

| Variable | Area (ha) | Total records | Last record year | Occupation duration | Sites within 1km | Sites within 2km | Sites within 3km |
|---|---|---|---|---|---|---|---|
| Area (ha) | | $0.331^{*}$ | $0.336^{*}$ | $0.297^{*}$ | 0.211 | 0.247 | 0.186 |
| Total records | $0.331^{*}$ | | $0.308^{*}$ | $0.596^{***}$ | $0.298^{*}$ | 0.230 | 0.199 |
| Last record year | $0.336^{*}$ | $0.308^{*}$ | | $0.358^{**}$ | $0.331^{*}$ | $0.305^{*}$ | 0.239 |
| Occupation duration | $0.297^{*}$ | $0.596^{***}$ | $0.358^{**}$ | | -0.017 | 0.077 | -0.023 |

## 4.4.6 Landscape Consolidation and Extirpation

The five new sites detected within known landscapes in 1970-76 ranks the partial decade joint-seventh out of 18 decades between 1798-1976 for which data are available. Although the species was unquestionably in decline by this point in time (Farrell, 1973), new sites were still being added less than six years before official extirpation. In 1976, an experienced butterfly recorder visited Ring Haw (southwest of Old Sulehay and east of Bedford Purlieus within the Fineshade network) as part of efforts to ascertain the status of *C. palaemon* in England following a tip-off by John Heath (former Head of the BRC) in 1975. The visit led to a solitary sighting and the only known *C. palaemon* record from the site (M. Fuller, personal communication). *C. palaemon* was also known to be present at Luffenham Heath in 1976 (Archer-Lock, 1982). Declaration of the butterfly's extirpation in England was, therefore, premature.

*C. palaemon* would have been altogether absent from England no earlier than 1977, however it may have persisted undetected for several years thereafter, perhaps on the border of Rutland and South Lincolnshire in the Stretton area, where it was still present at eight sites in the 1970s, along with an isolated sighting on a railway bank near Wing. Historic occupation of Coppice Leys and Culligalane Spinney southwest of Luffenham Heath was only uncovered in 2021 after handwritten entomological diaries referencing butterfly collecting trips were located in a museum archive during research for this project (Tozer, *c*. 1937-70; Bates, *c*. 1945-50). The Luffenham Heath sub-population and others within the Rutland landscape may have gone unnoticed due to their obscurity and ongoing poor understanding of historic butterfly distribution in the county (A. Russell, personal communication).

The private collection of a former Wiltshire butterfly recorder, Bowmont Weddell, featured at least one *C. palaemon*, as Weddell is known to have gifted a specimen of unknown provenance to a friend. The whereabouts of the specimen were last confirmed in 1991 (M. Fuller, personal communication). Bowmont's collection is thought to have been donated to 'Edinburgh Museum', however there are no records associated with either Bowmont or National Museums Scotland in our enhanced dataset. The true provenance of 287 specimens labelled 'Wansford' dated between 1831-1962 also remain unknown. It is doubtful the total number of sites known to have been occupied is representative of the actual number of sites that were occupied by *C. palaemon* at any given time in history, particularly in the 1800s. In 1828, the butterfly is noted to be in 'great plenty in many parts of Northamptonshire and Bedfordshire' (Stephens, 1828), however Clapham Park Woods is the only recorded Bedfordshire site until 1853.

## 4.5 Conclusions

We have demonstrated that the loss of *C. palaemon* in England was not as sudden as previously understood, and that the species' decline started at least a decade earlier in the late 1940s or early 1950s. This confirms the results found in Chapter Three. Metapopulation theory suggests that large woodland sites with correspondingly large colonies in England were likely more resistant to extirpation (e.g. Levins, 1969; Hanski, 1994; Schnell *et al.*, 2013), possibly until a combination of unsuitable woodland management, landscape change, and associated effects on connectivity ultimately rendered them uninhabitable. Through analysis of historic records to overcome spatiotemporal bias, we have suggested that increasing landscape impermeability after the 1940s, weakened site connectivity, and worsening habitat quality contributed to the loss of *C. palaemon* from England at some point after 1976. Efforts to restore woodland for *C. palaemon* in Rockingham Forest are already underway as part of an attempt to reestablish *C. palaemon* in the country. The provision of good quality habitat through wide woodland rides at large sites within networks with long histories of occupation (e.g. Fineshade Wood) should afford the species a foothold.

Number of records cannot be substituted for abundance in the case of a historic, extirpated species where a majority of data have been sourced from collected specimens. The bias of *C. palaemon* collectors to one populous site may have led to them ignoring another equally large colony a short distance away. The preferences of collectors created a clear bias in recording effort and historical data (e.g. two collectors took 95 *C. palaemon* from Skellingthorpe in 1956, which accounts for two-thirds of the wood's total records for that decade – see Figure 4.8). Conclusions should, therefore, be based on whether *C. palaemon* was detected at sites or not – particularly from the mid-1900s onwards – rather than numbers of records alone.

Although we can only speculate about abundance at sites, landscape consolidation (which was still occurring in the early 1970s, as evidenced by records from the Stretton metapopulation network) gradually improved the resolution of English *C. palaemon* distribution data. Once the butterfly was recorded at a site, the site then became amenable for detecting extirpation, even if records were sparse. An increase in recording (and perhaps abundance up to the 1940s) has ultimately enabled us to detect an earlier origin of decline of *C. palaemon* in England than was previously accepted, and also explain what may have driven it.

Given landscapes have become more fragmented since the 1970s, more work may need to be undertaken to improve their permeability. Wildlife corridors such as hedgerows, herb-rich field margins, roadside verges, and wildflower patches may increase the likelihood of *C. palaemon* expanding its range and naturally recolonising vacant sites. Deeper analysis of historic maps and other archives is required to better understand how corridors facilitated movement between core habitats. Creation of a patch occupancy model will indicate whether unoccupied sites within sub-landscapes were likely historically occupied and therefore compensate for absence of direct evidence. Findings could justify creation of dynamic habitat patches between Rockingham Forest woodland. Studies on the toxicity of insecticides and pesticides in agricultural and forestry settings on butterflies prior to the 1980s will also help to determine whether chemical use was another factor in the species' extirpation. New records that have met quality criteria for this study will now be disseminated to Butterfly Conservation County Recorders for verification before being accepted into the BNM dataset.

# 5

# Estimating Population Size, Movement, and Lifespan of a Reintroduced Butterfly Using Photographic Mark-Recapture

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## Abstract

The chequered skipper butterfly *Carterocephalus palaemon* was reintroduced to England in 2018 as part of a Butterfly Conservation-led, National Heritage Lottery-funded project known as Back from the Brink – Roots of Rockingham following several years of planning. Between 2019 and 2021, populations were sampled each May-June flight period by the lead author, timed count volunteers, Butterfly Conservation staff, and casual observers. A novel photographic mark-recapture (PMR) technique was trialled in conjunction with timed counts to determine whether individual *C. palaemon* specimens could be photo-identified through upperside wing markings and PMR established as a viable, non-invasive surrogate for mark-release-recapture (MRR) of a reintroduced butterfly species. Here, we discuss the differences in upperside wing markings of *C. palaemon* specimens, photo-identification methods, and best practice for capture-recapture in the field. We present findings on mobility and lifespan of the reintroduced population in England, use PMR data to generate annual population size estimates, and discuss the implications of the technique for population sampling of other Lepidopterans.

## 5.1 Introduction

Sampling techniques such as transect counts and MRR are essential tools for Lepidoptera conservation (e.g. Pollard, 1977, 1982; Taron and Ries, 2015; van Swaay *et al*., 2020). Butterflies, in particular, are visible indicators of the broader state of biodiversity, and presently the only invertebrate taxon for which population trends can be estimated in many parts of the world (e.g. de Heer *et al*., 2005; Thomas, 2005). As butterfly species are univoltine or multivoltine, the health of populations and impact of environmental change can be detected over short periods of time (Thomas, 2005; Rákosy and Schmitt, 2011; van Swaay and Warren, 2012). Photographic mark-recapture (PMR) is a non-invasive, inexpensive technique primarily used in marine biology to estimate abundance of Cetacea and Elasmobranchii (e.g. Rosel *et al.*, 2011; Fearnbach *et al.*, 2012; Gore *et al.*, 2016; Tubbs *et al.*, 2019). However, the potential of photo-identification in butterfly ecology has not yet been explored.

MRR is an established sampling technique that requires a butterfly to be captured in a net and its wings marked with ink (see Ehrlich and Davidson, 1960; Thomas, 1983b; Warren, 1983; Murphy *et al.*, 1986; Habel *et al.*, 2018; Williams *et al.*, 2018). MRR is invasive, time and resource-intensive, and unsuitable for endangered or sensitive species due to the uncertain risk of mortality, imperfect handling leading to mutilation, marking affecting mate selection and predation, and effect of disturbance on behaviour (e.g. Singer and Wedlake, 1981; Morton, 1982; Gall, 1984; Mallet, 1987). An experimental PMR technique was developed to estimate abundance of *C. palaemon*, which was declared extinct in England in 1976 after a precipitous decline beginning in the late 1940s-early 1950s (Wildman *et al.*, 2022) caused by coniferisation, coppicing abandonment, insufficient or inappropriate woodland management, afforestation, and other environmental and anthropogenic drivers (e.g. Farrell, 1973; Lamb, 1974; Peterken and Harding, 1974; Peterken, 1976; Collier, 1978, 1986; Warren, 1990; Ravenscroft, 1992, 1995; Moore, 2004). In 2018, the species was reintroduced to Fineshade Wood, Northamptonshire as part of a project led by Butterfly Conservation. Male and female adult butterflies were caught in the Fagne-Famenne region of Belgium, transported in refrigerated containers, and released at Fineshade Wood within 48 hours of capture. Further releases took place at the same site in 2019 and 2022.

PMR was preferred to MRR to avoid trampling narrow zones of vegetation occupied by the butterfly (and the wish to set a precedent to the large number of timed count volunteers on site), and due to low population density rendering traditional marking methods non-viable. Although found to be more labour-intensive than MRR, PMR provided a unique opportunity to utilise the large number of photographs taken of *C. palaemon* during three flight periods (2019-21) by the lead author, timed count volunteers, Butterfly Conservation staff, and casual recorders (hereafter referred to as personnel). Photographs are used in this chapter to annually estimate the size of the reintroduced population, and minimum lifespans (duration between initial and last capture) and flight distances of individual butterflies. In this study, we aim to determine the efficacy of PMR as a non-invasive alternative to MRR population sampling and discuss our findings in relation to the ecology of *C. palaemon* at Fineshade Wood. We also consider population size, individual butterfly movements and lifespan derived from this technique in relation to other studies of *C. palaemon*. Lastly, we briefly consider the potential for algorithm-based deep-learning PMR to assist with abundance, lifespan, and movement estimates for rare, endangered, or reintroduced butterfly species.

## 5.2 Methods

### 5.2.1 Population Sampling

An online worksheet was created by Back from the Brink – Roots of Rockingham Project Manager, Susannah O'Riordan, which was circulated by email to experienced butterfly surveyors who had expressed an interest in monitoring the *C. palaemon* population at Fineshade Wood. Personnel were able to edit the worksheet and input their names next to morning (1000-1300hrs) and/or afternoon (1300-1600hrs) slots for timed counts during 2019-21 flight periods. A map of 27 numbered rides was created by O'Riordan and split into sections. Ride maps were given to personnel along with UKBMS *C. palaemon* timed count recording forms (see Appendix Two, Figure A2.1). Personnel were allocated specific sections to walk to ensure coverage of the site was unbiased, and typically surveyed between 10-26 sections per day depending on how long they remained on site, their walking pace, and work rate.

During timed counts, on arrival at ride sections, a start time and the ride section code was written on recording forms. Rides were walked at a slow pace singularly or in pairs from the central turf zone to minimise habitat disturbance. When an adult *C. palaemon* was detected, the time was recorded, an eight or 10-figure OS grid reference taken, the individual sexed, its wing wear scored from four (perfect) to one (well-worn), and activity noted. Photographs were taken during encounters, however this was not attempted in all cases. Other target species and taxa of note were tallied in the species column or margins of forms. When the end of a ride section was reached, an end time, average wind speed and direction, percentage of sun, and temperature was recorded. Surveys were cancelled in the event of unsuitable weather. At the end of each flight period, O'Riordan created a dataset of *C. palaemon* sightings using data transcribed from UKBMS forms and casual records submitted through email from trusted surveyors. The forms were scanned and sent to the lead author so that survey effort and *C. palaemon* encounter rate per ride section could be calculated.

### 5.2.2 Photo-Identification

Personnel who encountered adult *C. palaemon* at Fineshade Wood were asked to photograph each specimen using a digital camera, smartphone, or other device capable of taking digital images, and send the file(s) along with time, date, location (eight or 10-figure OS grid reference), and ride section data. Image files were converted to .jpg format when necessary and titles reformatted in upper-case to contain the following information in this order: species, sex, ride section, dd/mm/yyyy, time, recorder name, image number (if multiple photos of the same encounter existed). Information for file names was obtained from image metadata and cross-referenced with recording forms and email correspondence to ensure accuracy. Occasionally, temporal metadata did not match times stated on recording forms. Inconsistencies were found to be due to personnel taking photos before or after recording encounters on monitoring forms, or photographic equipment being incorrectly configured. Anonymous photos, or photos from unverifiable sources without complete geospatial and temporal data that did not match any accepted records were excluded from analysis. Images were placed into folders according to year of sighting, then day and month sub-folders ready for cataloguing in the format dd/mm. Photos were then visually assessed in chronological order, and individual specimens identified through differences in upper-forewing (upf) and upper-hindwing (unh) markings.

A separate group of folders was created for catalogued photos (i.e. photos in which individual *C. palaemon* could be identified through unique wing patterns). A folder was created for each individual *C. palaemon* specimen, and given an alphanumeric code to represent the year (first two digits), specimen number (third and fourth digits), and sex (letter) (e.g. 1901M). A 'B' was added to codes of translocated 2019 Belgian specimens, which were marked with pen prior to release to differentiate them from the first generation of native English *C. palaemon*. Specimen codes were matched to *C. palaemon* records on the dataset originally created by O'Riordan. Image titles were not altered after cataloguing to ensure file provenance was preserved.

The variability of *C. palaemon* wing patterns, notably gold markings in the upf discal cell, and interspaces between subcoastal veins v10 and v4 in discal, postdiscal, and subapical wing areas enabled rapid photo-identification of individuals. Three key upf marking groups were examined for variation (zones marked with A, B, and C in Figure 5.1). Zone A (red triangle) was interpreted as a solid gold triangle with a void in its upper centre (if viewed from the same perspective as the image). This void was unique to each butterfly and considered the most useful upperside (ups) marking for identification due to the relative simplicity of its geometry. However, the geometry of markings in other zones – particularly B (green triangle) – were often as distinctive.

Markings in zones A, B, and C of Fineshade Wood *C. palaemon* survived wear, bleaching, and scale loss due to their high contrast with the brown base colour, size relative to the upf, and more proximal position than less distinct marginal markings. Some variation also existed on the underside (uns) of both the forewing and hindwing, however the uns was less frequently photographed due to the propensity of *C. palaemon* to rest in a wings-open posture. Unique markings on the uns were often sparser and less distinct than on the upf, and only keenly studied in the absence of upf markings or wing wear. Uns markings were much less distinctive for both sexes overall.

A high-resolution PC monitor was used to identify marking differences by eye. Images were manually compared side by side, reoriented, and photo-manipulated using Luminar (Skylum Software, 2020) to enhance contrast when necessary. Uns-only, blurred or otherwise poor-quality images were discarded and interpreted as missed capture events (equivalent to swinging a butterfly net at a target and failing to capture it) – equal to encounters where photography was not attempted at all. No photographs were taken of a number of *C. palaemon* sighted by personnel on timed counts during the three flight periods, however it was impossible to say whether those sightings were of retrospectively known captured or recaptured specimens, or new specimens that were never captured.

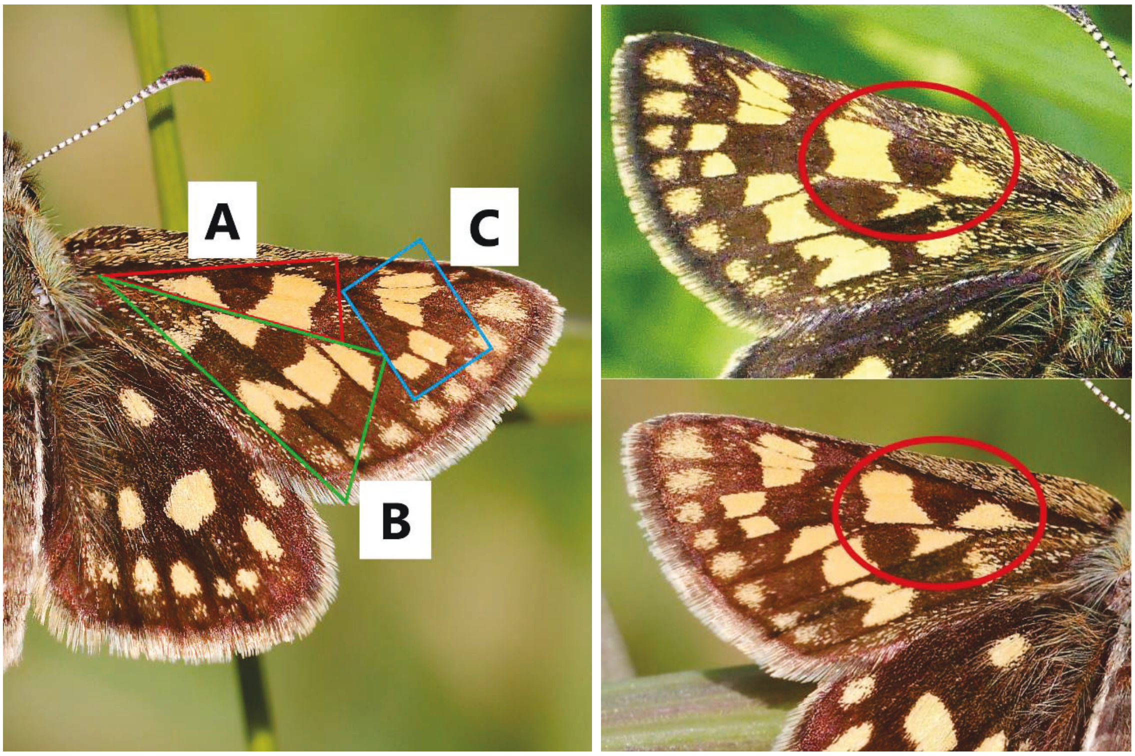


**Figure 5.1**: Images of *C. palaemon* with distinctive upper-forewing (upf) pattern zones highlighted (left) and examples of differences in upf markings of two individuals (top and bottom right) (Image credit: David James and Andy Wyldes)

## 5.2.3 Movements

Geospatial and temporal data from catalogued images were entered on to worksheets according to sighting year. Columns were titled as follows: ID (specimen code excluding sex), sex, total observations, minimal lifespan, capture one date, capture one time of day, GPS (eight or 10-figure OS grid reference). Observed lifespan was termed ‘minimum’ because the actual lifespan of recaptured individuals was always greater than duration the time between initial and last capture. No adult *C. palaemon* were observed from point of emergence to expiration, or recovered after they had expired. For recaptured specimens, the capture date, time of day, and GPS columns were repeated. Specimen codes, OS grid references, times and dates of recaptured specimens were exported to QGIS in .csv format. The FSC Biological Records Tool plugin (Field Studies Council, 2022) was used to plot data as circular 10m points (equivalent to an eight-figure OS grid reference) on a Google satellite map layer to standardise resolution. Straight line and ride measurements were taken from the middle of each ride (centre of the short turf zone), equidistant from bordering ditches, scrub zones, and woodland edge to negate inaccuracies in GPS data.

The QGIS Measure Line tool was used to measure straight line and ride-level movements. Straight line measurements were drawn as the crow flies from initial capture point to first recapture, from first recapture to second recapture, and so forth, irrespective of whether the line passed over woodland, hardcore tracks, or other linear features. Ride measurements were drawn by following the approximate centre of each ride section and turning 90° at junctions. In all cases, the shortest route that linked two points was chosen. This generated six variables: observed distance covered between any two points (straight line and ride), furthest observed distance from first capture point (straight line and ride), and cumulative observed distance covered between all points (straight line and ride).

Distances were inputted on an Excel worksheet with the following column headings: ID (specimen code without sex), sex, total captures, total recaptures, minimal lifespan, first capture date, first capture time, last capture date, last capture time, total distance covered (straight line and ride), maximum distance from first capture (straight line and ride), maximum distance covered between any two points (straight line and ride). Using these data, mean distance between captures, mean speed (straight line and ride in kilometres per hour), mean distance covered per hour (straight line and ride), and mean distance covered per day (straight line and ride) were calculated for each recaptured specimen. Combined means for all male and female specimens recaptured between 2019-21 were generated as well as separate means for males and females. Straight-line movements between captures were mapped in QGIS.

### 5.2.4 Abundance

Once images were processed and catalogued, the specimen codes of individual *C. palaemon* and their corresponding raw PMR data were converted to encounter histories on a worksheet with the following column headings: ID (specimen code minus sex), sex, and days in chronological order beginning with the date of first capture of first individual to the date of last capture of last individual. Where a specimen was captured or recaptured on a given date, a 'one' (captured or recaptured) or a 'zero' (not captured or recaptured) was entered into the relevant column. Encounter histories were then extracted to a plain text editor on which duplicate histories were combined and total duplicate histories entered at the end of each corresponding string followed by a semi-colon. For example, if four individuals had encounter histories that matched the one printed below, the row appeared as follows:

```
0001001100010000 4;
```

2019, 2020, and 2021 encounter histories were saved as separate .inp plain text files ready for import to Program MARK (White and Burnham, 1999) parameter estimation software. Data reformatting followed instructions available in Cooch and White (2017). The POPAN formulation – a parameterisation of the Jolly-Seber model (Schwarz and Arnason, 1996) within Program MARK – was used to generate capture probability, apparent survival rate, daily and super-population estimates. POPAN has been used to assess spatial and temporal dynamics in butterfly Batesian mimicry systems, study demographic processes in butterfly metapopulations, and estimate population size (Schtickzelle *et al*., 2002; Haddad *et al*., 2008; Prusa and Hill, 2021). Open populations of Cetacea and seals have also been monitored using POPAN (e.g. den Heyer *et al*., 2013; Galletti Vernazzani *et al*., 2017; Zeng *et al*., 2020). In Program MARK, .inp files for each flight period were selected, a title for the dataset inputted, and the number of encounter occasions increased to match the number of days the release site was monitored from first capture to last recapture. Time periods between each sampling occasion were changed to indicate monitoring intervals not equal to one day. In all cases, postponement of monitoring activity during flight periods was caused by unsuitable weather.

*C. palaemon* timed counts started before the first sighting and continued after the last sighting (as the last sighting was not able to be declared as such until after surveys ceased). Flight period was defined as the time period between first and last adult butterfly encounters (not captures and recaptures) in 2019, 2020, and 2021. Data from these time periods were used in all analyses and population size estimates. The number of covariates was left at one, and the appropriate data type chosen (e.g. POPAN). For POPAN, a numerical estimation run was executed by naming the run by study year and data type, and the model as POPAN – *p(*), phi(t), pent(t).* Where *p* was capture probability, *phi* was apparent survival, and *pent* was probability of entry. The parameter-specific link function was chosen for each analysis. Parameter Index Matrices (PIMs) were not respecified apart from *pent*, which was indicated to be zero by changing the according MLogit(1) link function values to MLogit(0) to reflect the fact that the founder population was a closed, single-site reintroduction with no probability of entry. The *N* super-population size estimate PIM was changed to Log. An output of parameter estimates including daily (*N-hat*) and gross population estimates (*N*-hat*) were generated and saved to a plain text file.

Daily POPAN population size estimates were tested against site-wide *C. palaemon* encounter rates using Spearman correlation in SPSS (IBM Corp., 2021) to establish whether statistically significant relationships existed between the variables. Encounter rates were generated by transcribing handwritten *C. palaemon* timed count data on to a worksheet. Total survey effort was calculated using minutes elapsed between the timed count start and finish time of each ride section. Total survey effort per day for all ride sections (in minutes) was divided by the total number of *C. palaemon* recorded that day to generate a base encounter rate *MinP* (number of survey minutes per encounter). The encounter rate was derived from all *C. palaemon* records, not just photo-identified specimens. Additional daily and gross population size estimates used a bisection of the Craig model (Craig, 1953) in Craig Estimator 2.0 (Sebek and Sebek, 2019) for computation. All plots were created in Microsoft Excel (Microsoft Corporation, 2021). In 2019, 24 Belgian specimens were released at Fineshade Wood to supplement the first generation of native English *C. palaemon*. This quantity was not added to estimated abundance for 2019. No PMR data were available from the 2018 reintroduction year.

## 5.3 Results

### 5.3.1 Capture-Recapture Rates

Over the three flight periods (2019-21), 72 individual *C. palaemon* were photo-identified (i.e. captured) using PMR (Table 5.1). Of these 72 individuals, 30 (41.7%) were recaptured (i.e. identified from a photograph taken during a subsequent encounter) and 47 movements were detected (Figure 5.2). A total of 298 *C. palaemon* records were submitted by personnel, meaning that 24.2% of all recorded *C. palaemon* were captured. A higher ratio of males than females were captured (1.77:1) and recaptured (2.33:1) across the three flight periods. One in five (20.2%) *C. palaemon* recorded in 2019 were captured. This percentage rose to 26.7% in 2020 and 32.3% in 2021. Of captured individuals, almost a third (31.4%) were recaptured in 2019. This increased to over half (56.3%) in 2020 but fell slightly to 47.6% in 2021. Total records declined markedly in 2020 and 2021 compared to 2019 (-65.3% and -62.4%, respectively), but this was not mirrored by an equivalent decrease in total captured specimens (-54.3% in 2020 and -40.0% in 2021). Total recaptured specimens remained stable despite the variance in total records submitted across the three flight periods. The ratio of captures to missed captures decreased with each successive flight period. However, it must be noted that there was no attempt to photograph every *C. palaemon* encountered. Wing wear data were considered too sparse to be of use in this study due to the small quantity of recapture data available and good to very good condition of a majority of recaptured individuals (Figure 5.3).

**Table 5.1**: Total *C. palaemon* records, photographic-mark-recapture (PMR) captures and recaptures, 2019-21. For every *C. palaemon* that was able to be photo-identified in 2019, 3.34 were not. By 2021, this ratio had narrowed to only 1.48 missed captures for every positive photo-identification.

| Year | Total records | Total captured | Total missed captures | Capture-missed capture ratio | Female-male capture ratio | % of total records | Total recaptured | Female-male recapture ratio | % of total recaptured |
|---|---|---|---|---|---|---|---|---|---|
| 2019 | 173 | 35 | 117 | 1:3.3 | 1:1.7 | 20.2 | 11 | 1:2.7 | 31.4 |
| 2020 | 60 | 16 | 31 | 1:1.9 | 1:1.7 | 26.7 | 9 | 1:3.0 | 56.6 |
| 2021 | 65 | 21 | 31 | 1:1.5 | 1:2.0 | 32.3 | 10 | 1:3.3 | 47.6 |

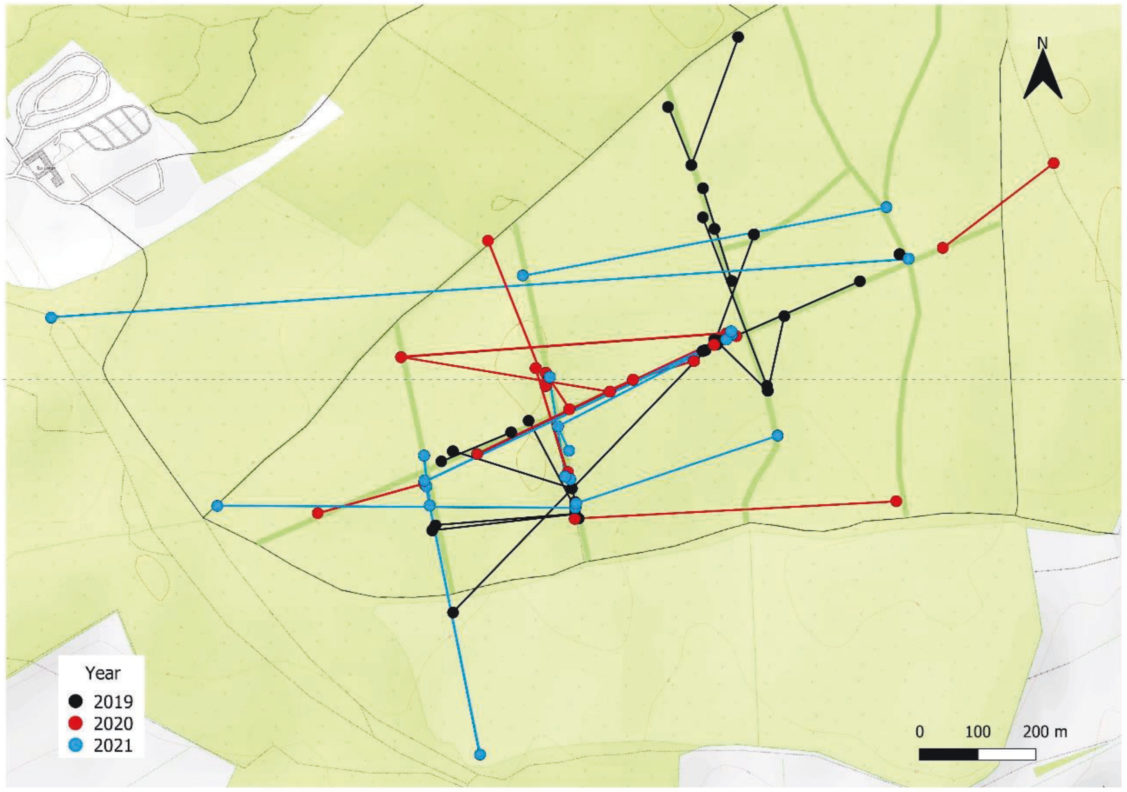


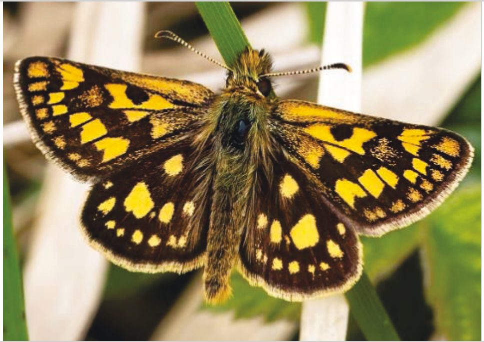
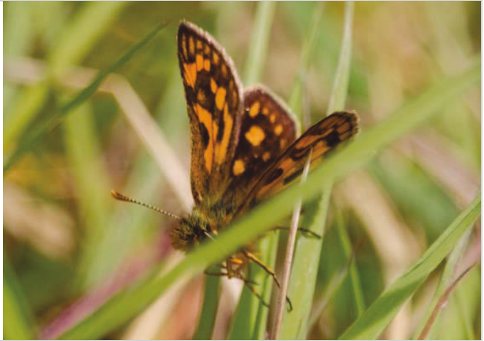
**Figure 5.2**: Photographic-mark-recaptured male and female *C. palaemon* movements at Fineshade Wood, 2019-21 (n=47). Each point represents an eight or 10-figure OS grid reference at which an individual was captured or recaptured. Straight lines connect points in order from initial capture to last recapture.

| Code | Capture | Recapture |
|---|---|---|
| 1901F |  |  |
| 1902M |  |  |
| 1903M |  |  |
| 1904M |  |  |
| 1905F |  |  |

| | | |
|---|---|---|
| 1905M |  |  |
| 1907MB |  |  |
| 1908M |  |  |
| 1909FB |  |  |
| 1910M |  |  |

| | | |
|---|---|---|
| 1919M |  |  |
| 2001F |  |  |
| 2002F |  |  |
| 2002M |  |  |
| 2003F |  |  |

| | | |
|---|---|---|
| 2005M |  |  |
| 2006M |  |  |
| 2007M |  |  |
| 2008M |  |  |
| 2009M |  |  |

| | | |
|---|---|---|
| 2101F |  |  |
| 2101M |  |  |
| 2102M |  |  |
| 2103F |  |  |
| 2103M |  |  |

| | | |
|---|---|---|
| 2104F |  |  |
| 2105M |  |  |
| 2106M |  |  |
| 2109M |  |  |
| 2112M |  |  |

**Figure 5.3**: 2019-21 Fineshade Wood *C. palaemon* capture-recapture example photographs to illustrate the unique markings of each butterfly. Note how individuals can still be positively identified even when in poor condition (e.g. 2101M, 2105M).

Thirteen specimens were recaptured more than once, ten were recaptured twice, two were recaptured three times, and one 2019 female (1901F) was recaptured four times over a 290-hour (12 day) minimum lifespan (Figure 5.4). Minimum lifespans of eight of the 30 recaptured specimens exceeded 96 hours. Two specimens (2008M and 2104F) were recaptured only 17 and 32 minutes after initial capture and not photo-identified again. Elapsed time between captures was rounded down to the nearest whole hour, therefore the minimum lifespan of 2008M and 2104F was stated as zero. The minimum lifespan of 13 of the 30 (43.3%) recaptured individuals was 24 hours or less. Five of these 13 were captured and recaptured on the same day.

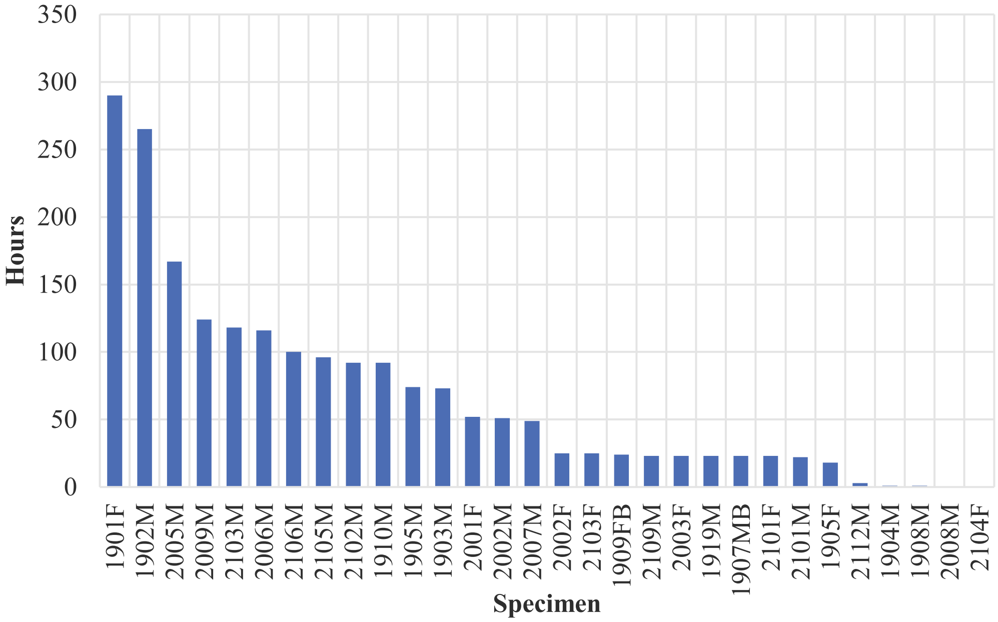
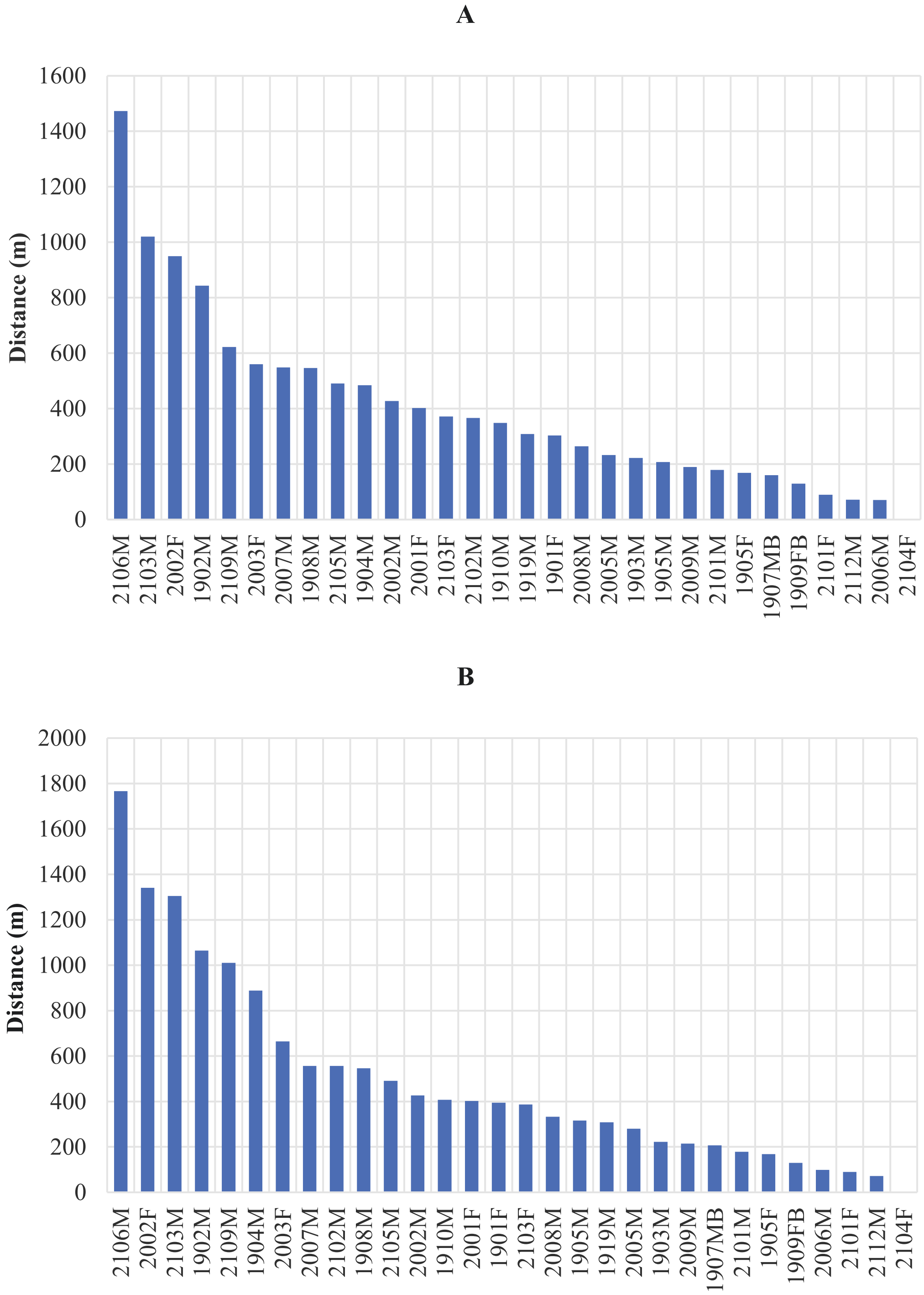


**Figure 5.4**: The minimum lifespan of each photo-recaptured *C. palaemon* between 2019-21 at Fineshade Wood in hours (i.e. elapsed time between initial capture and last recapture).

## 5.3.2 Movements and Lifespan of Individual Butterflies

The mean minimum lifespan of all recaptured *C. palaemon* across the three flight periods was 66 hours (59 hours for males and 68 hours for females). Mean minimum lifespan for male and female *C. palaemon* decreased from 80 hours in 2019 to 67 hours in 2020 and 50 hours in 2021. Based on straight-line measurements between all capture points, two specimens (2106M and 2103M) were indirectly observed to have travelled a total distance >1,000m (Figure 5.5). However, using ride-level measurements, five specimens were calculated to have travelled >1,000m in total. The maximum indirectly observed distance travelled was 1,473m using straight-line measurements and 1,766m using ride-level measurements by 2106M. The male was only recaptured once, over 100 hours after initial capture. Large total distances were not achieved solely over multiple days: distances of 664m, 1,010m, and 1,341m were covered by three specimens (2002F, 2003F, and 2109M) in a mean time of 24 hours, as determined by ride-level measurements. One specimen, 1904M, was measured to have travelled 888m in one hour.



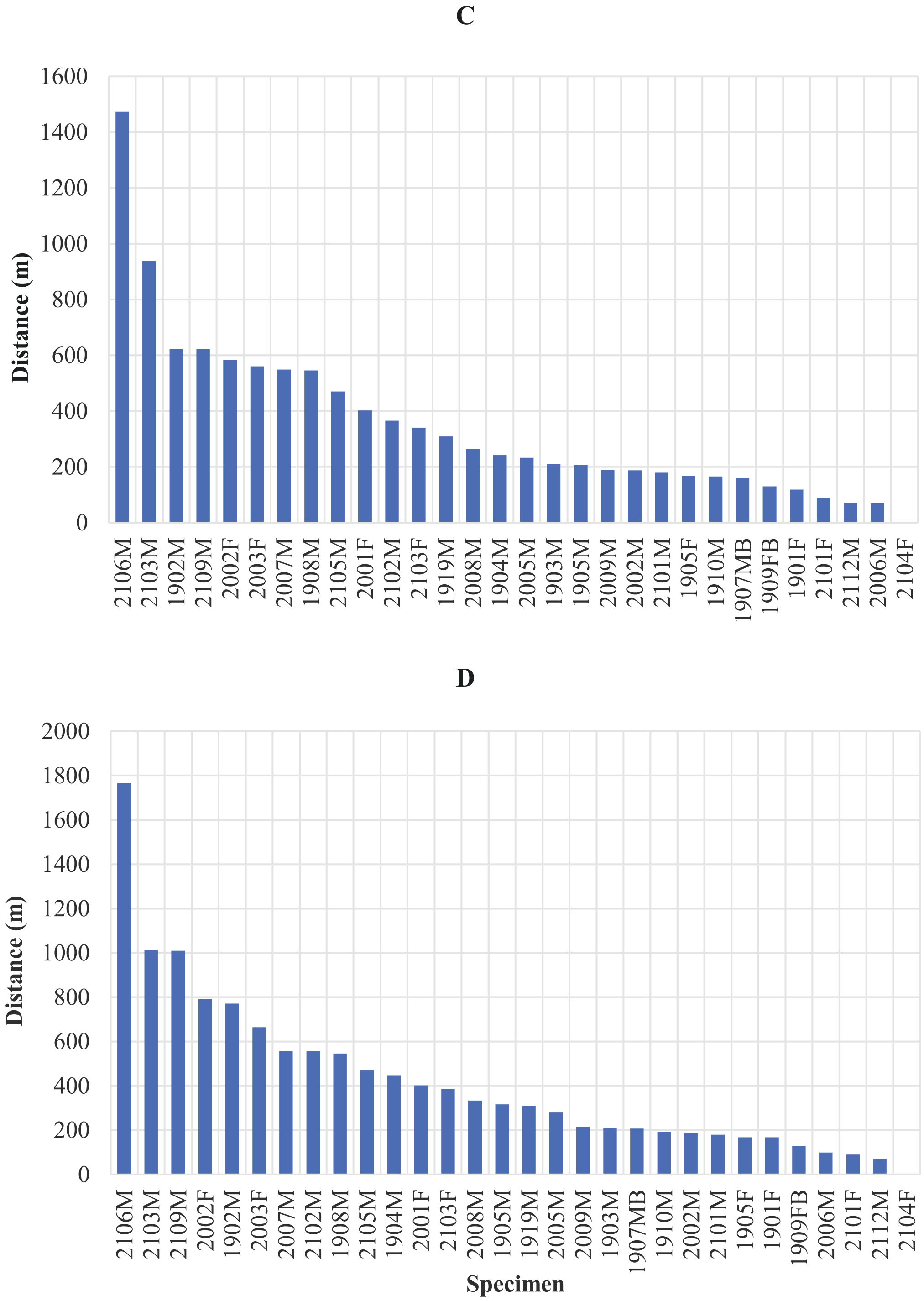
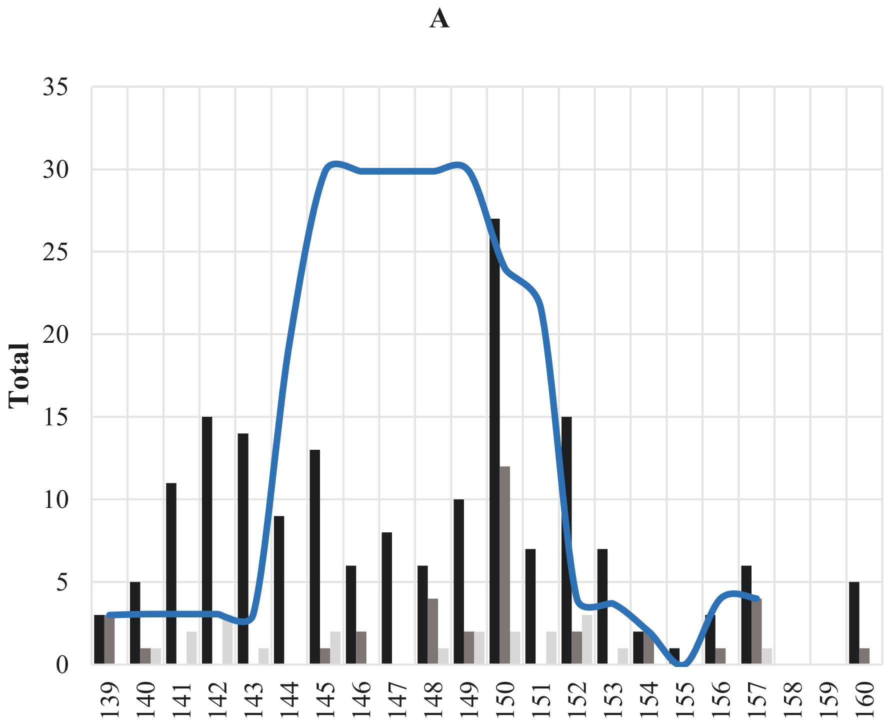


**Figure 5.5**: Total distance covered by 2019-21 photo-recaptured *C. palaemon* at Fineshade Wood – A) straight line and B) ride-level, and furthest distance from initial capture – C) straight line and D) ride-level. Note the high mobility of 2106M using all metrics.

### 5.3.3 Capture-Recapture Trends

In 2019, capture abundance peaked the same day as the population peak (i.e. most *C. palaemon* encounters recorded in a single day) with a total of 27 sightings and 12 captures on Julian day 150 (Figure 5.6). Recaptures otherwise remained low and stable during the flight period, never exceeding three per day. There were no captures between days 141 and 144 despite the fact that recorded *C. palaemon* encounters reached double figures on days 141, 142, 143, and 145. Individuals recaptured during this time period (four total) were captured during the first two days of the flight period. Captures peaked on the same day as the population peak in 2020, along with recaptures. On day 140, 13 *C. palaemon* were recorded and three individuals captured – the same number of individuals that were captured the preceding day. Daily capture-recapture totals remained low throughout the shorter 2020 and 2021 flight periods (17 and 21 days, respectively) but remained comparable to 2019 barring its peak day of 12 captures. A mean 1.6 captures occurred per day in 2019 compared to 1.0 in both 2020 and 2021. For recaptures, 1.0 occurred per day in 2019, compared to 0.8 in 2020 and 0.6 in 2021. In 2021 the season was declared over by day 164 and monitoring activities suspended, however a casual survey on day 167 resulted in a *C. palaemon* encounter that extended the observed flight period.



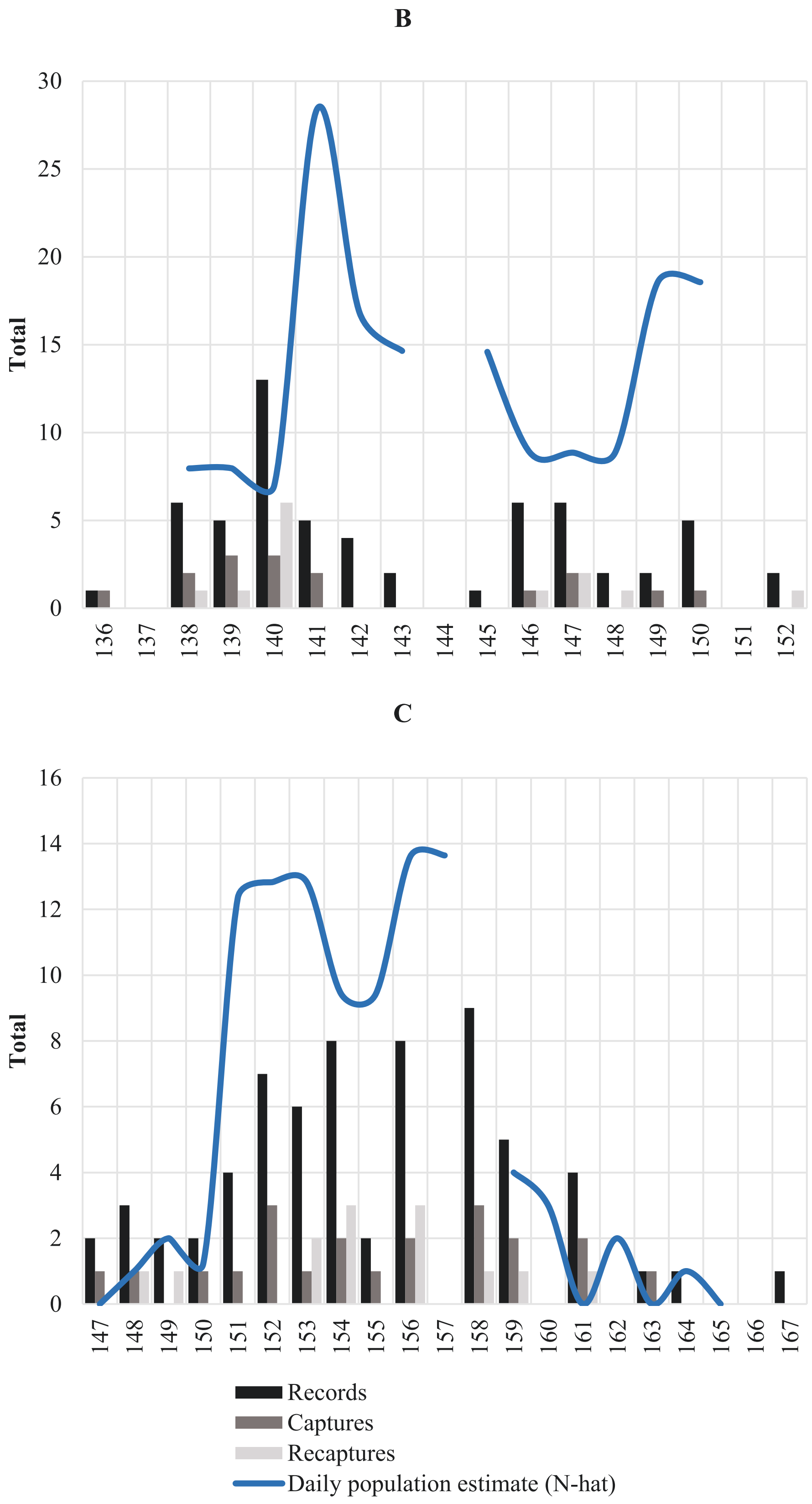


**Figure 5.6**: Flight period records, photographic captures and recaptures, and POPAN model daily population size estimates (*N-hat*) per Julian day for A) 2019, B) 2020, and C) 2021 (note differences in horizontal and vertical axis scaling).

### 5.3.4 Population Size Estimates and Tests of Association

The POPAN model indicated a sharp increase in abundance early in all flight periods, rising sixfold between days 143-144 in 2019, fourfold between days 140-141 in 2020, and tenfold between days 149-150 in 2021 (see Tables 5.2, 5.3, and 5.4). A classic bell-shaped curve was generated by the model between days 143-152 in 2019, which was expected given the butterfly's short flight period, but this was not replicated in either 2020 or 2021. Model estimates lag behind actual increases in observations early in 2019 and 2020 but pre-empt an increase towards the population peak in 2021. Elapsed time per *C. palaemon* encounter was lower in 2019 and 2020 (a mean of 67 minutes and 125 minutes, respectively) than 2021, where elapsed time per encounter rose to 292 minutes. Survey effort declined in 2020 as a consequence of COVID-19 movement restrictions but recovered in 2021. Daily population size estimates did not vary proportionally with the difference in total survey effort between the two flight periods.

The POPAN model estimated gross population size *N*-hat* to have been 314 individuals in 2019, which increased to 332 in 2020, and then more than doubled to 721 in 2021 (Table 5.5). Elapsed time per encounter per day *MinP*, encounters per minute per day *Pmin*, and total records per day *Rec* were tested against POPAN daily population size estimates *N-hat* for each flight period using Spearman correlation in SPSS (IBM Corp., 2021). Data from each flight period were then combined to provide an overall measure of association for the 2019-21 study period. A total of 80 tests of association were carried out between variables and 32 found to be statistically significant. In 2019, only a significant moderate negative *r*-value was found between *N-hat* and *MinP* (elapsed time per encounter) ($r$=-0.460, ρ=0.041). Very highly significant ρ-values and moderate positive *r*-values were found between *N-hat* (daily population size estimate) and *Pmin* (encounters per minute per day) ($r$=0.470, ρ=<0.001), and *N-hat* and *Rec* (total records per day) ($r$=0.439, ρ=0.001) when 2019-21 data were combined.

Paired sampled t-tests were performed with combined years *N-hat* correlated variables (*Pmin*: t=7.629, ρ=<0.001 and *Rec*: t=3.413, ρ=0.001). We therefore rejected the null hypothesis $H_0$ that there was no relationship between population size estimate and both encounter rate and total records per day. Relationships between *N-hat* and *Pmin* were expected to be positive (higher frequency of *C. palaemon* encounters per minute coupled with higher population size estimate) and relationships between *N-hat* and *MinP* inverse (greater elapsed time per *C. palaemon* encounter resulting in lower population size estimate). No significant *r*-values were found between any of the variables in 2020, however in 2021, a very highly significant, strong positive *r*-value was found between *N-hat* and *Rec* ($r$=0.698, ρ=0.001).

**Table 5.2**: 2019 Fineshade Wood *C. palaemon* flight period survey effort, encounter rate, and daily POPAN model population estimate per Julian day.

| Julian day | Survey effort (mins) | Total records | Time per encounter (mins) | Daily population estimate (*N-hat*) | 95% lower CI | 95% upper CI | *N-hat* standard error (SE) | Daily Craig population estimate (*N*) |
|---|---|---|---|---|---|---|---|---|
| 139 | 280 | 3 | 93.33 | 3.00 | 1.09 | 8.27 | 1.66 | N/A |
| 140 | 381 | 5 | 76.20 | 3.06 | 1.11 | 8.44 | 1.70 | 11 |
| 141 | 523 | 11 | 47.55 | 3.06 | 1.11 | 8.44 | 1.70 | 6 |
| 142 | 505 | 15 | 33.67 | 3.06 | 1.11 | 8.44 | 1.70 | 4 |
| 143 | 717 | 14 | 51.21 | 3.06 | 1.11 | 8.44 | 1.70 | 4 |
| 144 | 248 | 9 | 27.56 | 19.39 | 0.01 | 25,855.39 | 16,372.16 | N/A |
| 145 | 907 | 13 | 69.77 | 29.88 | 14.69 | 60.78 | 11.19 | 5 |
| 146 | 150 | 6 | 25.00 | 29.88 | 14.69 | 60.78 | 11.19 | 8 |
| 147 | 453 | 8 | 56.63 | 29.88 | 14.69 | 60.78 | 11.19 | N/A |
| 148 | 328 | 6 | 54.67 | 29.88 | 14.69 | 60.78 | 11.19 | 14 |
| 149 | 502 | 10 | 50.20 | 29.88 | 14.69 | 60.78 | 11.19 | 17 |
| 150 | 489 | 27 | 18.11 | 24.00 | 6.05 | 95.28 | 19.20 | 40 |
| 151 | 506 | 7 | 72.29 | 21.57 | 0.05 | 10,064.52 | 2,941.49 | 38 |
| 152 | 596 | 15 | 39.73 | 4.00 | 1.66 | 9.65 | 1.89 | 39 |
| 153 | 180 | 7 | 25.71 | 3.70 | 0.01 | 1,875.65 | 577.10 | 38 |
| 154 | 366 | 2 | 183.00 | 2.00 | 0.59 | 6.78 | 1.38 | 42 |
| 155 | 154 | 1 | 154.00 | 0.00 | 0.51 | 0.51 | N/A | N/A |
| 156 | 0 | 3 | 0.00 | 4.00 | 1.66 | 9.65 | 1.89 | 44 |
| 157 | 852 | 6 | 142.00 | 4.00 | 1.66 | 9.65 | 1.89 | 52 |
| 160 | 628 | 5 | 125.60 | 1.00 | 0.20 | 5.03 | 0.99 | 55 |

**Table 5.3**: 2020 Fineshade Wood *C. palaemon* flight period survey effort, encounter rate, and daily POPAN model population estimate per Julian day.

| Julian day | Survey effort (mins) | Total records | Time per encounter (mins) | Daily population estimate (*N-hat*) | 95% lower CI | 95% upper CI | *N-hat* standard error (SE) | Daily Craig population estimate (*N*) |
|---|---|---|---|---|---|---|---|---|
| 136 | 0 | 1 | 0.00 | 1.00 | 0.20 | 5.04 | 0.99 | N/A |
| 138 | 240 | 6 | 40.00 | 7.96 | 0.40 | 158.80 | 24.28 | 7 |
| 139 | 280 | 5 | 56.00 | 7.96 | 2.36 | 26.82 | 5.45 | 13 |
| 140 | 260 | 13 | 20.00 | 7.00 | 3.63 | 13.48 | 2.41 | 12 |
| 141 | 256 | 5 | 51.20 | 28.39 | 10.35 | 77.86 | 15.64 | 16 |
| 142 | 265 | 4 | 66.25 | 16.83 | 0.09 | 3,277.34 | 626.31 | N/A |
| 143 | 42 | 2 | 21.00 | 14.65 | 0.08 | 2,817.17 | 535.89 | N/A |
| 145 | 92 | 1 | 92.00 | 14.59 | 0.08 | 2,803.35 | 533.03 | N/A |
| 146 | 340 | 6 | 56.67 | 8.85 | 2.79 | 28.11 | 5.71 | 17 |
| 147 | 934 | 6 | 155.67 | 8.85 | 2.79 | 28.11 | 5.71 | 19 |
| 148 | 964 | 2 | 482.00 | 8.85 | 2.79 | 28.11 | 5.71 | 19 |
| 149 | 727 | 2 | 363.50 | 18.56 | 4.80 | 71.70 | 14.48 | 20 |
| 150 | 303 | 5 | 60.60 | 18.56 | 4.80 | 71.70 | 14.48 | 22 |
| 152 | 288 | 1 | 288.00 | 18.51 | 0.36 | 958.87 | 0.36 | 22 |

**Table 5.4**: 2021 Fineshade Wood *C. palaemon* flight period survey effort, encounter rate, and daily POPAN model population estimate per Julian day.

| Julian day | Survey effort (mins) | Total records | Time per encounter (mins) | Daily population estimate (*N-hat*) | 95% lower CI | 95% upper CI | *N-hat* standard error (SE) | Daily Craig population estimate (*N*) |
|---|---|---|---|---|---|---|---|---|
| 147 | 1,180 | 2 | 590.00 | 1.00 | 0.20 | 5.00 | 0.98 | N/A |
| 148 | 872 | 3 | 290.67 | 2.00 | 0.60 | 6.70 | 1.36 | 3 |
| 149 | 1,042 | 2 | 521.00 | 1.23 | 0.00 | 771.16 | 271.83 | 3 |
| 150 | 1,478 | 2 | 739.00 | 12.35 | 12.36 | 12.36 | 0.00 | 4 |
| 151 | 970 | 4 | 242.50 | 12.83 | 6.34 | 25.97 | 4.77 | 7 |
| 152 | 1,354 | 7 | 193.43 | 12.83 | 6.34 | 25.97 | 4.77 | 17 |
| 153 | 903 | 6 | 150.50 | 9.42 | 4.04 | 21.98 | 4.27 | 14 |
| 154 | 1,110 | 8 | 138.75 | 9.42 | 4.04 | 21.98 | 4.27 | 14 |
| 155 | 774 | 2 | 387.00 | 13.61 | 13.60 | 13.60 | 0.00 | 17 |
| 156 | 966 | 8 | 120.75 | 13.64 | 6.18 | 30.10 | 5.74 | 18 |
| 158 | 1,475 | 9 | 163.89 | 4.00 | 1.69 | 9.45 | 1.84 | 23 |
| 159 | 1,561 | 5 | 312.20 | 3.00 | 1.11 | 8.14 | 1.63 | 27 |
| 160 | 613 | 0 | 0.00 | 0.00 | 0.39 | 0.39 | 0.00 | N/A |
| 161 | 580 | 4 | 145.00 | 2.00 | 0.60 | 6.70 | 1.36 | 30 |
| 162 | 359 | 0 | 0.00 | 0.00 | 0.26 | 0.26 | 0.00 | N/A |
| 163 | 633 | 1 | 633.00 | 1.00 | 0.20 | 5.00 | 0.98 | 32 |
| 164 | 552 | 1 | 552.00 | 0.00 | 0.36 | 0.35 | 0.00 | N/A |
| 167 | 79 | 1 | 79.00 | 0.00 | 0.73 | 0.73 | 0.00 | N/A |

**Table 5.5**: 2019-21 Spearman correlation coefficients for POPAN *C. palaemon* population estimates against *C. palaemon* encounter rate, total records per day, elapsed time per encounter per day, and Craig model daily population estimates (***ρ=<0.001, **ρ=<0.01, *ρ=<0.05).

| Year | Gross population estimate (*N*-hat*) | Standard error (SE) | Variable | Elapsed time per encounter per day (*MinP*) | Encounters per minute per day (*Pmin*) | Daily population estimate (*N-hat*) | Total records per day (*Rec*) | Craig population estimate (*N*) |
|---|---|---|---|---|---|---|---|---|
| 2019 | 314.32 | 4.32x10$^{5}$ | *MinP* | | -0.714$^{***}$ | -0.460$^{*}$ | -0.531$^{*}$ | -0.009 |
| | | | *Pmin* | -0.714$^{*}$ | | 0.430 | 0.742$^{***}$ | -0.218 |
| | | | *N-hat* | -0.460$^{*}$ | 0.430 | | 0.383 | -0.006 |
| | | | *Rec* | -0.531$^{*}$ | 0.742$^{***}$ | 0.383 | | -0.123 |
| | | | *N* | -0.009 | -0.218 | -0.006 | -0.123 | |
| 2020 | 332.27 | 1.09x10$^{6}$ | *MinP* | | -0.600$^{*}$ | 0.436 | -0.293 | 0.604$^{*}$ |
| | | | *Pmin* | -0.600$^{*}$ | | -0.035 | 0.638$^{*}$ | -0.292 |
| | | | *N-hat* | 0.436 | -0.035 | | -0.233 | 0.428 |
| | | | *Rec* | -0.293 | 0.638$^{*}$ | -0.233 | | 0.120 |
| | | | *N* | 0.604$^{*}$ | -0.292 | 0.428 | 0.120 | |
| 2021 | 721.08 | 3.38x10$^{6}$ | *MinP* | | -0.405 | 0.135 | -0.098 | 0.125 |
| | | | *Pmin* | -0.405 | | 0.386 | 0.698$^{***}$ | 0.364 |
| | | | *N-hat* | 0.135 | 0.386 | | 0.730$^{***}$ | 0.578$^{*}$ |
| | | | *Rec* | -0.098 | 0.698$^{***}$ | 0.730$^{***}$ | | 0.603$^{**}$ |
| | | | *N* | 0.125 | 0.364 | 0.578$^{*}$ | 0.603$^{**}$ | |
| All | N/A | N/A | *MinP* | | -0.574$^{**}$ | -0.175 | -0.354$^{*}$ | 0.128 |
| | | | *Pmin* | -0.574$^{***}$ | | 0.470$^{***}$ | 0.702$^{***}$ | 0.842 |
| | | | *N-hat* | -0.175 | 0.470$^{***}$ | | 0.439$^{***}$ | 0.248 |
| | | | *Rec* | -0.354$^{*}$ | 0.702$^{***}$ | 0.439$^{***}$ | | 0.030 |
| | | | *N* | 0.128 | 0.842 | 0.248 | 0.030 | |

## 5.4 Discussion

### 5.4.1 Mobility, Dispersal, and *C. palaemon* Population Size at Fineshade Wood

We have demonstrated that PMR is an effective way to determine the movements and minimum lifespan of individual butterflies, however some daily population size estimates (particularly in 2020) have large standard errors (SE) as site coverage was insufficient. The total number of personnel officially permitted to access the reintroduction site in 2020 due to COVID-19 social distancing restrictions was six. Personnel surveyed ride sections for up to 16 combined hours per day (not including total time spent on site) for over two weeks, however density and frequency of coverage per day was compromised by an overall lack of site presence. The actual start of the 2020 flight period was likely missed, as access rights were granted two days after a local resident observed one *C. palaemon* during a casual survey.

In the first reintroduction year, 2018, 42 adult *C. palaemon* (32 females and 10 males) were released at Fineshade Wood. If *N*-hat* (POPAN gross population size estimate) for 2019 (314 individuals) is accepted on the basis of the significant moderate negative *r*-value between *N-hat* and *Pmin* ($r$=-0.460, ρ=0.041), then gross abundance of English *C. palaemon* in 2019 increased 648.4% from 2018. A further 24 *C. palaemon* (12 males and 12 females) were translocated from Belgian donor sites in May 2019 whilst the first-generation native *C. palaemon* was on the wing. Gross population size in 2019 was therefore estimated to have been 338.

The lack of statistically significant *N-hat* correlations with other variables in 2020 suggests daily population size estimates should be treated with caution. Based on *C. palaemon* minimum lifespans from 2019-21 (a maximum of 296 hours and mean of 66 hours), 2020 *N-hat* population peak declined too rapidly for the estimate to be reliable. No significant correlations with *Pmin* or *MinP* were found in 2021, however a very highly significant ρ-value and strong positive *r*-value between *N-hat* and *Rec* (number of *C. palaemon* records per day) ($r$=0.730, ρ=<0.001) indicated a degree of model compatibility with real-world abundance. The 2021 *N-hat* population peak lasted for a series of days rather than increasing and decreasing rapidly as in 2020. A minor depression in *N-hat* on day six of the flight period was immediately followed by an increase in abundance that exceeded the earlier estimated peak. Paucity of capture-recapture data was again considered responsible for unlikely estimates towards the end of the flight period.

Population estimates from the Jolly-Seber method (of which POPAN is a parameterisation) are thought to be reliable if more than 9% of the total population is sampled and the survival rate from one sampling period to the next is not less than 0.5 (Bishop and Sheppard, 1973). If we assume that the consistency of gross 2019-20 POPAN estimates of 338 (including reinforcements from Belgium) and 332 signal reliability, 31 *C. palaemon* would need to have been sampled in 2019 to reach the 9% minima. We captured 35 individuals (11.1%), sampled the site daily, and know that individual butterflies can live for up to 17-18 days (Ravenscroft, 1992). Given 42 *C. palaemon* were released at Fineshade Wood in 2018, the 2019 population would need to have need to have increased tenfold to >406 for POPAN estimates to be unreliable (<91% of the total population sampled). Although only 16 *C. palaemon* were captured in 2020 (3.9% of 406), known population size in the 2018 reintroduction year provided a baseline against which subsequent model estimates could be tested for accuracy.

Conventional MRR studies have shown populations are much higher than casual observations demonstrate (e.g. Thomas, 1983a; Warren, 1983) (see Chapter Three), however intensive sampling has proved capturing up to 50% of a population present on one day when numbers are low is possible (Brereton, 1997). At Fineshade Wood, sampling was intensive and regularly exceeded 16 hours per day during the first two weeks of the 2021 flight period, therefore *N*-hat* for 2021 (721.08) seems illogical given the low encounter rate versus previous flight periods despite similarities in recapture rate. However, bearing mobility of the reintroduced population and therefore dispersal potential in mind (three individuals were recaptured >1km from initial capture location), it is conceivable individuals flew beyond the monitored site boundary in extremely low densities and remained undetected for the duration of their adult lifespans. This may explain declining encounter rates on the most intensively sampled ride sections in successive years. Two 2021 specimens (2106M and 2106F – the latter a female that was not recaptured) were detected in woodland edge habitat >430m from regularly sampled ride sections. The male, 2106M, was encountered during wider reconnaissance by one volunteer, which lead to 2106F being recorded in the same patch the following day.

During MRR studies of the Scottish population of *C. palaemon*, Ravenscroft (1992) observed unmarked individuals “flying through the rides in the plantation […] out onto open moorland, a distance of 1km or more.” He also encountered females “in situations unsuitable to support populations” several kilometres away from recognised colonies, and one female was seen flying over 6km from a known site. We have found *C. palaemon* behaves in a manner that belies its reputation as a low mobility species since its reintroduction to England. Mean distance between captures and maximum recorded movements of *C. palaemon* at Fineshade Wood are greater than at Chambers Farm Wood, Lincolnshire (Moore, 2004) and Ariundle, Scotland (Ravenscroft, 1992). Furthest movement recorded over one day or greater at Ariundle was 549m for males and 197m for females, and 410m at Chambers Farm Wood by both a male and a female. However, at Fineshade Wood, using straight line measurements for accurate comparison to Scottish movements, 2109M covered 622m in 23 hours and 2002F covered 950m in 25 hours.

As discussed, maximum distances travelled at Fineshade Wood are much larger still (see Tables 5.6 and 5.7). Smaller sample size (Ravenscroft captured 66 individuals with movement data spanning one day or greater compared to our 17) but larger maximum movements detected at Fineshade Wood compared to Ariundle (1,473m and 549m, respectively) are accounted for by our larger, but more intensively sampled survey area. This is shown in mean movement between captures over one day or greater, which was 98m for males and 79m for females at Ariundle and 126.3m for males and 305.6m for females at Fineshade Wood. Based on our findings, we argue *C. palaemon* should not be described as sedentary. Maximum duration between initial and last capture at Ariundle was 17 days (Ravenscroft, 1992), however at Fineshade Wood a maximum duration (i.e. minimum lifespan) of 12 days was recorded. Moore (2004) saw the number of marked individuals decline rapidly in Chambers Farm Wood after two days using MRR, similar to the mean minimum lifespan observed at Fineshade of 66 hours using PMR.

**Table 5.6**: Ride-level movements (in metres) and minimum lifespan (in hours) of 2019-21 photo-recaptured *C. palaemon* at Fineshade Wood.

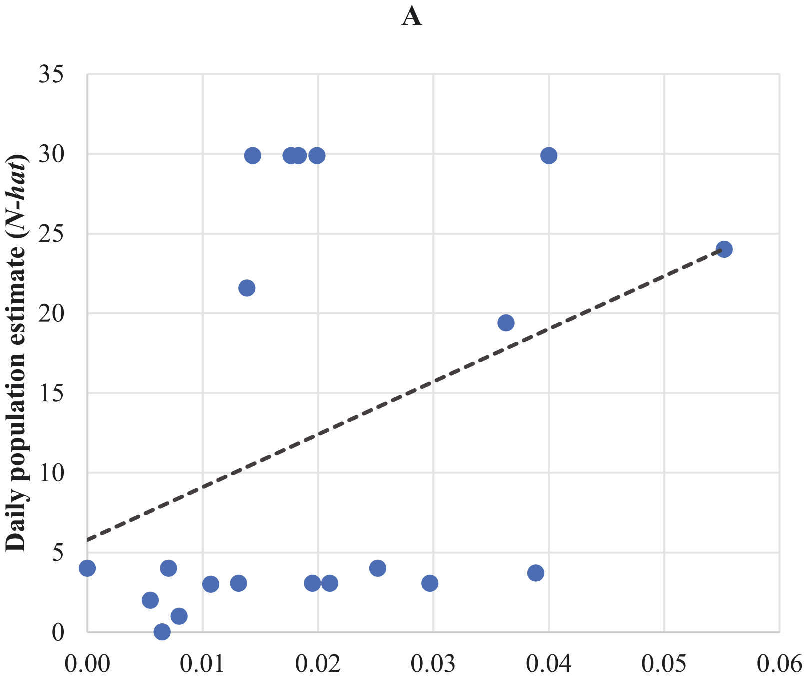
| Specimen code | Total captures | Minimum lifespan (hours) | Total distance covered (m) | Maximum distance from first capture (m) | Maximum distance between captures (m) | Mean distance between captures (m) | Mean distance per hour (m) | Mean distance per day (m) |
|---|---|---|---|---|---|---|---|---|
| 1901F | 5 | 290 | 395 | 168 | 178 | 98.8 | 1.4 | 33 |
| 1902M | 4 | 265 | 1,064 | 771 | 771 | 355 | 4 | 96 |
| 1903M | 3 | 73 | 222 | 210 | 210 | 111 | 3 | 73 |
| 1904M | 3 | 1 | 888 | 446 | 446 | 444 | 888 | N/A |
| 1905F | 3 | 18 | 168 | 168 | 95 | 84 | 9.3 | 224 |
| 1905M | 3 | 74 | 316 | 316 | 316 | 158 | 4.3 | 102 |
| 1907MB | 2 | 23 | 207 | 207 | 207 | 207 | 9 | N/A |
| 1908M | 2 | 1 | 546 | 546 | 546 | 546 | 546 | N/A |
| 1909FB | 2 | 24 | 130 | 130 | 130 | 130 | 5.4 | 130 |
| 1910M | 3 | 92 | 408 | 191 | 300 | 204 | 4.4 | 106 |
| 1919M | 2 | 23 | 309 | 310 | 309 | 309 | 13.4 | N/A |
| 2001F | 3 | 52 | 402 | 402 | 299 | 201 | 7.7 | 186 |
| 2002F | 4 | 25 | 1,341 | 791 | 773 | 447 | 53.6 | 1,287 |
| 2002M | 3 | 51 | 427 | 188 | 239 | 214 | 8.4 | 201 |
| 2003F | 2 | 23 | 664 | 664 | 664 | 664 | 28.9 | N/A |
| 2005M | 2 | 167 | 280 | 280 | 280 | 280 | 1.7 | 40 |
| 2006M | 2 | 116 | 99 | 99 | 99 | 99 | 0.9 | 20 |
| 2007M | 2 | 49 | 557 | 557 | 557 | 557 | 11.4 | 273 |
| 2008M | 2 | 0 | 333 | 333 | 333 | 333 | N/A | N/A |
| 2009M | 2 | 124 | 215 | 215 | 215 | 215 | 1.7 | 42 |
| 2101F | 2 | 23 | 90 | 179 | 179 | 179 | 3.9 | N/A |
| 2101M | 2 | 22 | 179 | 90 | 90 | 90 | 8.1 | N/A |
| 2102M | 2 | 92 | 557 | 557 | 557 | 557 | 6.1 | 145 |
| 2103F | 3 | 25 | 387 | 387 | 343 | 194 | 15.5 | 372 |
| 2103M | 3 | 118 | 1,305 | 1,013 | 807 | 653 | 11.1 | 265 |
| 2104F | 2 | 0 | 0 | 0 | 0 | 0 | N/A | N/A |
| 2105M | 3 | 96 | 491 | 471 | 481 | 246 | 5.1 | 123 |
| 2106M | 2 | 100 | 1,766 | 1,766 | 1,766 | 1,766 | 17.7 | 424 |
| 2109M | 2 | 23 | 1,010 | 1,010 | 1,010 | 1,010 | 43.9 | N/A |
| 2112M | 2 | 3 | 72 | 72 | 72 | 72 | 24 | N/A |
| *Mean* | *2.6* | *66* | *494* | *418* | *409.1* | *347.5* | *62* | *218* |

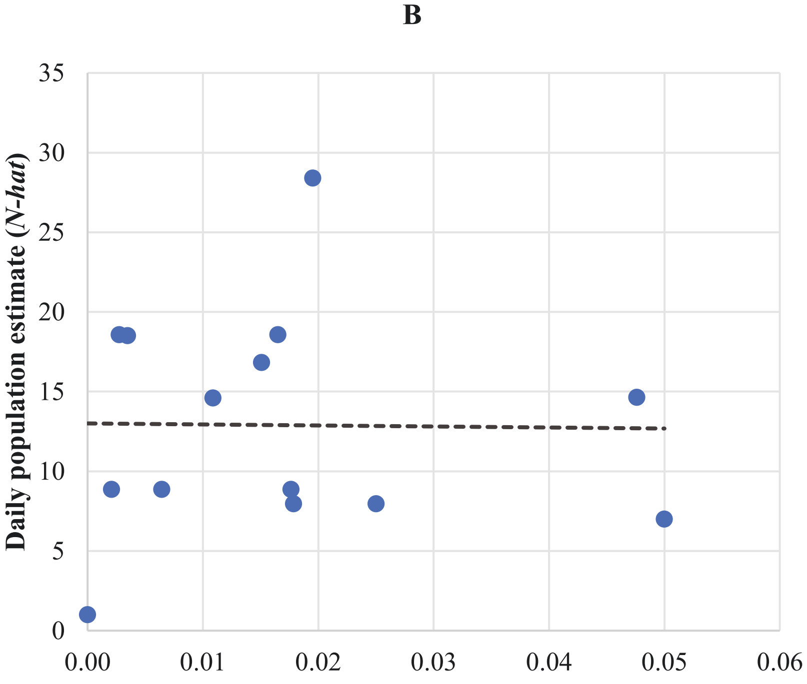
**Table 5.7**: Straight-line movements (in metres) and minimum lifespan (in hours) of 2019-21 photo-recaptured *C. palaemon* at Fineshade Wood.

| Specimen code | Total captures | Minimum lifespan (hours) | Total distance covered (m) | Maximum distance from first capture (m) | Maximum distance between captures (m) | Mean distance between captures (m) | Mean distance per hour (m) | Mean distance per day (m) |
|---|---|---|---|---|---|---|---|---|
| 1901F | 5 | 290 | 303 | 119 | 134 | 75.8 | 1 | 25.1 |
| 1902M | 4 | 265 | 843 | 622 | 622 | 281 | 3.2 | 76.3 |
| 1903M | 3 | 73 | 222 | 210 | 210 | 111 | 3 | 73 |
| 1904M | 3 | 1 | 484 | 242 | 242 | 242 | 484 | N/A |
| 1905F | 3 | 18 | 168 | 168 | 95 | 84 | 9.3 | N/A |
| 1905M | 3 | 74 | 207 | 207 | 207 | 104 | 2.8 | 67.1 |
| 1907MB | 2 | 23 | 160 | 160 | 160 | 160 | 7.0 | N/A |
| 1908M | 2 | 1 | 546 | 546 | 546 | 546 | 546 | N/A |
| 1909FB | 2 | 24 | 130 | 130 | 130 | 130 | 5.4 | 130 |
| 1910M | 3 | 92 | 349 | 166 | 241 | 175 | 3.8 | 91 |
| 1919M | 2 | 23 | 309 | 309 | 309 | 309 | 13.4 | N/A |
| 2001F | 3 | 52 | 402 | 402 | 299 | 201 | 7.7 | 185.5 |
| 2002F | 4 | 25 | 950 | 584 | 566 | 317 | 38 | 912 |
| 2002M | 3 | 51 | 427 | 188 | 239 | 214 | 8.4 | 200.9 |
| 2003F | 2 | 23 | 560 | 560 | 560 | 560 | 24.3 | N/A |
| 2005M | 2 | 167 | 233 | 233 | 233 | 233 | 1.4 | 33.5 |
| 2006M | 2 | 116 | 71 | 71 | 71 | 71 | 0.6 | 14.7 |
| 2007M | 2 | 49 | 549 | 549 | 549 | 549 | 11.2 | 268.9 |
| 2008M | 2 | 0 | 264 | 264 | 264 | 264 | N/A | N/A |
| 2009M | 2 | 124 | 189 | 189 | 189 | 189 | 1.5 | 36.6 |
| 2101F | 2 | 23 | 179 | 179 | 179 | 179 | 3.9 | N/A |
| 2101M | 2 | 22 | 90 | 90 | 90 | 90 | 8.1 | N/A |
| 2102M | 2 | 92 | 366 | 366 | 366 | 366 | 4 | 95.5 |
| 2103F | 3 | 25 | 372 | 341 | 328 | 186 | 14.9 | 357.1 |
| 2103M | 3 | 118 | 1,020 | 939 | 618 | 510 | 8.6 | 207.5 |
| 2104F | 2 | 0 | 0 | 0 | 0 | 0 | N/A | N/A |
| 2105M | 3 | 96 | 491 | 471 | 481 | 246 | 5.1 | 122.8 |
| 2106M | 2 | 100 | 1,473 | 1,473 | 1,473 | 1,473 | 14.7 | 353.5 |
| 2109M | 2 | 23 | 622 | 622 | 622 | 622 | 27 | N/A |
| 2112M | 2 | 3 | 72 | 72 | 72 | 72 | 24 | N/A |
| *Mean* | *2.6* | *66* | *402* | *349* | *336.5* | *285.3* | *45.8* | *182.9* |

## 5.4.2 Validating Conventional Sampling Methods

Although significant coefficients between *N-hat*, *Pmin*, and *MinP* were not found for all flight periods individually, when years were combined, a very highly significant ρ-value and moderate positive *r*-value was found between *N-hat* and *Pmin* (*r*=0.470, ρ=<0.001) (Figure 5.7). This suggests broad agreement between daily encounter rates and POPAN daily population size estimates – a relationship weakened when years are analysed in isolation due to a lack of quantitative data. The integrity of PMR data is dependent on high butterfly abundance, intensive population sampling, and low missed capture rates. Missed captures occurred at a rate of 67.6% in 2019, 51.7% in 2020, and 33.3% 2021. Continued rate reduction through adoption of the monitoring methods outlined in this chapter will enhance PMR success in future flight periods. As encounter rate (a variable independent of PMR, generated through timed counts) is correlated with population size estimates generate *through* PMR, we can have confidence in the ability of less labour-intensive sampling methods such as timed counts to generate accurate population size estimates (see Thomas, 1983b), but only when sufficient quantitative data are available. This is evidenced by the strength of correlations when data from 2019-21 flight periods are combined, which compensates for insufficient sample size in individual years.





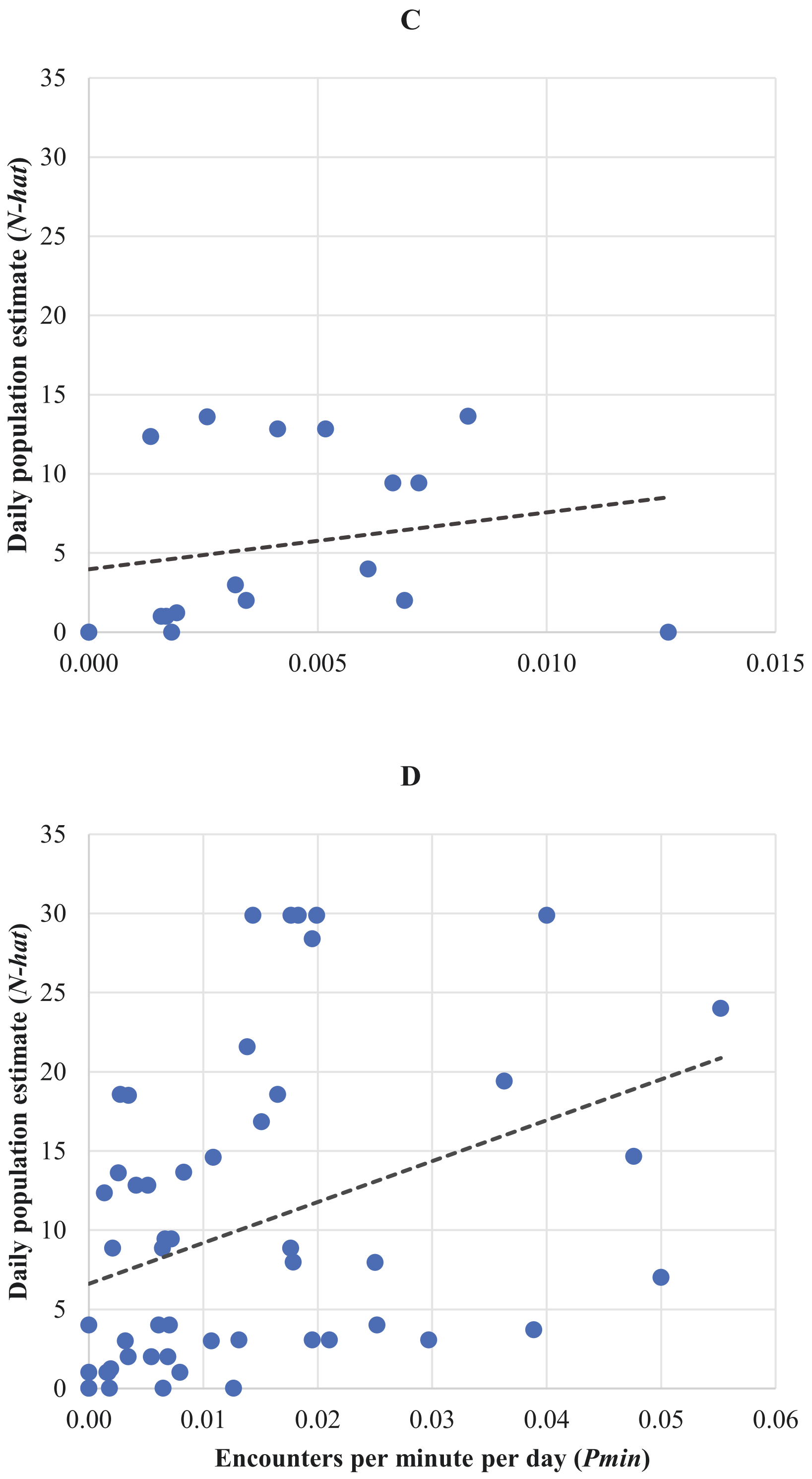


**Figure 5.7**: A) 2019 (*r*=0.430, ρ=0.059), B) 2020 (*r*=-0.035, ρ=0.905), C) 2021 (*r*=0.386. ρ=0.114), and D) 2019-21 (*r*=0.470*,* ρ=<0.001) combined POPAN daily *C. palaemon* population size estimates (*N-hat*) plotted against encounters per minute per day at Fineshade Wood (*Pmin*) (note differences in x-axis scaling). Note the absence of a statistically significant relationship in separate years (A, B, and C) compared to when 2019-21 data were combined.

### 5.4.3 The Benefits of Photographic Mark-Recapture

MRR has been used to estimate abundance for a range of Lepidoptera species (e.g. Brereton, 1997; Nowiciki *et al.*, 2005; Vlasanek *et al.*, 2013; Williams *et al.*, 2018) since the technique was first developed in 1896 (Southwood and Henderson, 2000). However, opinion on the impact of capture to recapture probability, wing damage caused by handling, and effect of marking on predation and mating behaviour is varied and uncertain (e.g. Ehrlich and Davidson, 1960; Singer, 1981; Morton, 1982; Gall, 1984). Experimental approaches to monitor populations of rare and endangered butterflies have been tested, including models of seasonal flight phenologies derived from transect counts (presence-absence surveys) (Haddad, 2008). Although transect counts are cost-effective and non-invasive, they do not account for individual detection probability and temporal fragmentation of adult butterfly populations (Nowicki *et al.*, 2008).

International guidelines for standardised butterfly monitoring recommend transect counts and fruit bating (van Swaay *et al.*, 2015), and consider MRR impractical due to high labour cost and handling requirements. MRR sampling has been optimised to improve cost-effectiveness of population size estimates (Turlure *et al.*, 2017), however the protocol is altogether incompatible with a reintroduced butterfly species of characteristically low density and detectability. An experimental approach to estimate population size is therefore required for sensitive butterfly reintroduction projects and endangered Lepidoptera species – one which utilises opportunistic photographic data, conventional MRR methodology, and the potential of non-specialists to sample butterfly populations in a non-invasive way.

The PMR population sampling described in this chapter retains the quality of data obtained through MRR whilst digitally preserving specimens for photo-identification – a process equivalent to capture and marking. Although PMR for Lepidoptera is limited in application to species with unique markings and a propensity to rest with wings open, wing wear and damage is butterfly and moth-specific, and could be used to differentiate more uniformly or subtly patterned species. PMR is especially relevant to rare, endangered, or recently reintroduced populations given it is non-invasive and lacks the potential to influence behaviour (e.g. Singer and Wedlake, 1981; Morton, 1982, 1984; Gall, 1984; Mallet, 1987). Suggested criteria for adoption of PMR or MRR sampling methods is presented in Table 5.8. High-resolution photography has been used to identify microhabitats for grassland butterfly species in agricultural landscapes (Habel *et al.*, 2018), however the capabilities of modern handheld photographic equipment have not yet been fully explored in butterfly ecology.

**Table 5.8**: Suggested criteria for adoption of photographic mark-recapture (PMR) and mark-release-recapture (MRR) population sampling methods.

| Sampling method | Criteria for adoption |
|---|---|
| Photographic mark-recapture (PMR) | Species has unique ups wing or thoracic markings<br>Species rests in a wings-open posture<br>Habitat damage is likely using MRR and considered detrimental<br>Species population density is low<br>Species is rare, endangered, or reintroduced<br>Capture and handling of specimens is considered an unacceptable risk<br>A large number of volunteers with cameras are present |
| Mark-release-recapture (MRR) | Species has indistinct ups wing or thoracic markings<br>Species rests in a wings-closed posture<br>Habitat damage is unlikely or not considered detrimental<br>Species population density is high<br>Species is common or abundant where found<br>Capture and handling of specimens is not considered an unacceptable risk<br>A small number of volunteers or no volunteers are present |

## 5.4.4 Best Practice for Photographic Mark-Recapture

*C. palaemon* timed count photographers became more adept at independently photo-identifying and sexing individuals as the project progressed, and in doing so improved the cost-effectiveness of the cataloguing process. *C. palaemon* are small (29-31mm), fast-flying butterflies that are difficult to sex in the field even when at rest. Female clubs at the tip of antennae are yellow-orange with a black base, whereas male clubs are solid yellow and more brightly coloured. However, each butterfly must be viewed head-on for sexing, ideally with close-focusing binoculars. This viewing angle, whilst helpful for sexing, is a poor perspective for photo-identification purposes. Specimens often behaved unpredictably – males regularly took flight to intercept passing invertebrates and defend territory – therefore ups photography must be prioritised over sexing in order to prevent missed captures.

Sexing *C. palaemon* is best performed in the field as image quality, white balance, hue, contrast, and colouration can differ between photographic equipment depending on camera/smartphone model and settings. Subtle differences between the brighter, bolder wing markings of the male ups and duller, paler markings of the female ups are often lost in photographs. Abdomen width and length in both sexes can be deceptive – apparent dimensions can vary according to viewing angle, wear, and whether females are egg-laden. Sexing using apparent morphological variance in photographs is therefore not recommended due to unreliability. Personnel should survey in pairs during *C. palaemon* PMR sampling, with one prioritising ups photography, and the other with sexing via antennae clubs. Sexing of known individuals can be safely bypassed and a ups photo taken for recapture verification during later cataloguing. Minor inaccuracies in recording encounter time of day and position arising as a consequence of favouring PMR data collection have little material impact on movement and minimum lifespan analyses. Image cataloguing for 2019-21 was carried out after each flight period. Rapid processing and circulation of images of captured individuals whilst *C. palaemon* is still on the wing may enable survey personnel to familiarise themselves with distinctive wing markings and/or wear and aid active recapture in the field, further improving the cost-effectiveness of this technique.

It may be important that specimens are captured shortly after emergence. Mallet (1986) has shown the majority of movements of red postman *Heliconius erato* occurred before first capture, leading to gross underestimates of mobility. Some butterfly studies (e.g. Warren, 1987) highlight differences in mobility between sexes. Ravenscroft (1992) states Scottish populations of *C. palaemon* may be dynamic, with females being 'mobile and spread over the countryside' and both sexes emerging 'well away from recognised flight area[s].' His observations indicate 'butterflies will move several hundred metres after emergence before settling' and that those emerging away from core habitat will fly to the nearest suitable area. If this is also true for English *C. palaemon*, specimens captured in suboptimal condition – implying greater age – may already have moved large distances undetected, leading to mobility underestimates. For instance, if the capture of 2106M in pristine condition was missed, its sole observed movement to a location 1,473m away (using straight-line measurement) four days later would be unknown. Capturing fresh specimens may, therefore, lead to higher and/or more reliable mobility estimates. Related to this, identifying larval sites and ride sections where females congregate for oviposition could increase the likelihood of fresh *C. palaemon* captures during the following flight period.

## 5.5 Conclusions

We trialled an experimental PMR sampling technique for estimating abundance, mobility, and minimum lifespan of a reintroduced population of butterfly species found in low densities. This non-invasive approach enabled us to determine the movements and minimum lifespan of individual butterflies. The potential of PMR as a technique for generating data for daily abundance and gross population estimates using capture-recapture models has also been demonstrated. Modern biological recording already encourages citizen scientists to submit casual sightings of Lepidoptera to databases using smartphone apps such as iRecord (UKCEH, 2022a) and iRecord Butterflies (UKCEH, 2022b) and attach photographs of encounters for verification by experts such as County Recorders. Algorithm-based deep-learning technologies have improved in the past decade (LeCun *et al.*, 2015). Tools such as ObsIdentify (Observation International, 2022), Google Lens (Google LLC, 2022), and Seek (California Academy of Sciences and National Geographic Society, 2022) use artificial intelligence (AI) to analyse digital images for automatic species photo-identification in the field, however determination accuracy is limited by image quality, rarity, and mutilation of specimens (Molls, 2021).

Researchers have developed a computer vision timeline known as Mothra that is able to detect species, set scale, determine specimen orientation, measure wing features, and identify the sex of >180,000 digitised butterfly museum specimens in a controlled environment (Genov, 2017; Wilson *et al.*, 2022). A photo-identification study of captured african death's-head hawkmoth *Acherontia atropos* that uses Automatic Photo Identification Suite (APHIS) software to detect differences in thoracic colour patterns has also been successful (Ruiz de la Hermosa *et al.*, 2022). The dorsal fins, facial features, and symmetry of common bottlenose dolphins *Delphinus truncates* have been used for photo-identification and computer-assisted methods developed for the species (Mazzoil *et al.*, 2004; Thompson *et al.*, 2019). Software such as DISCOVERY (Gailey and Karczmarski, 2012) can assist with management and cataloguing of photographs, but not automatic identification.

Given the rate of progress in the field of algorithm-based photo-identification, development of artificial intelligence (AI) capable of identifying individual butterflies through photographs will improve cost-efficiency of PMR sampling of *C. palaemon* populations and other rare and endangered Lepidoptera with unique wing markings. Large quantities of photographic data will result in detailed capture-recapture histories which can be used by formulations such as POPAN to generate reliable population size estimates and related parameters. This will enhance non-invasive insight into the ecology of *C. palaemon* – particularly mobility, lifespan, and habitat preference of individual butterflies, and the status of colonies in Rockingham Forest.

# 6

# The Ecology of the Chequered Skipper Butterfly *Carterocephalus palaemon* at Fineshade Wood, England

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## Abstract

As a case of a species being reintroduced to a country within its indigenous range several decades after extirpation, understanding of the ecology of the chequered skipper butterfly *Carterocephalus palaemon* in England is relatively poor. Although the butterfly's behaviour in Scotland and Europe is well documented, there is scant information on native historic English populations. *C. palaemon* has been reintroduced to Fineshade Wood in England using founders from the Fagne-Famenne region of Belgium. The basic ecology and traits of non-native *C. palaemon* in England are, therefore, unknown, and must be documented to enable comparisons to extant Scottish and European populations. Here, we describe the butterfly's relationship to primary nectar source bugle *Ajuga reptans*, adult diurnal activity and roosting preference, and how *C. palaemon* utilises ride structure for flight navigation. We found that female encounter rate is positively related to *A. reptans* abundance and density, and that low nectar availability but high butterfly abundance indicates certain microhabitats may facilitate behaviours other then nectaring, such as oviposition. Our results suggest that *C. palaemon* may be capable of spatial memory and route learning in line with other butterfly species to assist with navigation, foraging, and territorial perching. Lastly, lowered energy demands through opportunistic roosting on grass blades after spells of dormancy may be related to *A. reptans* presence. We anticipate our findings improving adult detection rates, informing habitat management in Rockingham Forest, and leading to further studies of the importance of linear features such as hedgerows and field margins to *C. palaemon* in England.

## 6.1 Introduction

In this chapter, we offer insight into the ecology of *C. palaemon* at Fineshade Wood since the species' reintroduction to England in 2018. As we demonstrate, the butterfly is generally well understood in Europe and elsewhere in the UK, however some aspects of its behaviour are poorly documented. Here, diurnal activity is described, along with the male and female butterfly's relationship to nectar plant bugle *Ajuga reptans.* Using data supported by field observations made from 2019-21, we offer insight into how *C. palaemon* utilises its habitat for a variety of behaviours such as roosting, thermoregulation, conveyance, and territory defence. We also detail the microhabitat of six larvae discovered during 2019 searches and highlight issues with tracking females. We create a reference for *C. palaemon* ecology at Fineshade Wood that can be used to improve detectability, anticipate behaviour, and better understand the ecological requirements of the adult butterfly in England.

### 6.1.1 Nectar Plants and Butterfly Preference

Butterfly species have different floral preferences, and visit flowers of certain colours more than others (e.g. Ômura and Honda, 2005; Tiple *et al.*, 2005; Kandori and Yamaki, 2012; Santhosh and Basavarajappa, 2016). Plant category and corolla type have also been found to influence butterfly visitation at nectar plants (Subedi *et al.*, 2020). Nectar is rich in amino acids, and butterflies prefer nectar with high amino acid content, which enhances fecundity (Mevi-Schutz and Erhardt, 2005). *C. palaemon* is known to prefer blue and purple flowers such as *A. reptans*, which is one of the butterfly's primary nectar sources (e.g. Frohawk, 1934; Collier, 1966; Houston, 1976; Hockey, 1978; Kelly, 1983; Collier, 1986; Warren, 1990; Ravenscroft, 1992; Moore, 2004) (Figure 6.1). *A. reptans* is an erect perennial with purple-tinged flowers and blue corollas that grows up to 30cm. The plant can be found in damp woodland clearings, coppice woodland, scrub, hedge banks, and unimproved grassland up to 760m throughout Britain (Streeter *et al*., 2016). *A. reptans* is abundant where found at Fineshade Wood, most frequently in short turf zones of wide, annually mown rides.

**Figure 6.2**: ♀ (female) *C. palaemon* nectaring on a flower at the top of a bugle *Ajuga reptans* spike at Fineshade Wood.

*C. palaemon* nectaring behaviour changes according to plant species. For those with deep corolla tubes such as *A. reptans* and bluebell *Hyacinthoides non-scripta*, feeding adults must "lunge characteristically" into flowers, but can feed from the edge of more open flower heads such as marsh thistle *Cirsium palustre* (Ravenscroft, 1992). Female *C. palaemon* nectar vigorously and have been observed gathering in patches of *A. reptans* and *C. palustre* growing on wet, richer soils amongst rushes *Juncus* spp. or willow *Salix* spp. scrub (Ravenscroft, 1994a; Ravenscroft and Warren, 1996). Adult male and female *C. palaemon* behaviour is characterised by lengthy periods of nectaring interspersed with short flights between flower visitations, with moments of basking before and after flight (Ravenscroft, 1992).

At Ariundle in Scotland, female *C. palaemon* express a strong preference for *A. reptans* and are more likely to be seen visiting the plant than males, which are much less specific (Ravenscroft, 1992; Ravenscroft, 1994a; Ravenscroft and Warren, 1996). In sections 6.3.1 and 6.4.1, we will determine whether female *C. palaemon* at Fineshade Wood are associated with *A. reptans* in the same way as Scottish females. Male abundance will also be tested against *A. reptans* spike abundance and density per ride section to establish whether floral preference of both sexes at Ariundle is replicated in English habitat.

### 6.1.2 Detectability and Vegetation Utilisation

*C. palaemon* activity has been recorded between 0900-1900hrs during adult flight periods, with a peak in observations between 1400-1600hrs (Ravenscroft, 1992). However, information on diurnal activity in England is scarce. Apparently, *C. palaemon* "should be sought from seven to nine 'o' clock in the morning", when it "play[s] in pairs just after sunrise, or at least as soon as the morning fog has evaporated" (Abbot, 1798). We will define a time period of diurnal activity and peak hours of observations in England using adult *C. palaemon* timed count data and casual records from 2019, 2020, and 2021 at Fineshade Wood. Anecdotal evidence suggests a brief decline in activity around midday or early afternoon. In section 6.4.2 of this chapter, we will confirm whether speculated changes in detectability associated with this time of day are supported by data, or whether observer bias is responsible for a perceived reduction in sightings.

Male *C. palaemon* are energetic butterflies which aggressively defend territory by pinging from high perches to intercept other flying invertebrates. Collier (1986) notes the use of tall herbage such as bracken *Pteridium aquilinum* and *C. palustre* as vantage points. Males are highly responsive and known to chase large insects such as dragonflies as well as investigate shadows cast by birds flying overhead. In the absence of perceived trespassers, they patrol in short flights from perch to perch or in longer, circular flights around territories – typically sunny nooks in sheltered woodland edges (Ravenscroft, 1992; Thomas and Lewington, 2016). Male *C. palaemon* perching and territorial behaviour is linked to mate location. Males will passively wait for females to fly through territory, or patrol and actively search for them in a manner consistent with other hesperids (e.g. Scott 1973a, 1973b, 1974; Hockey, 1978; Thomson, 1980; Kelly, 1983; Collier, 1986; Dennis and Williams, 1987; Dennis and Shreeve, 1988).

### 6.1.3 *C. palaemon* Ecology in Scotland and Northern Europe

*C. palaemon* can live up to three weeks, but average lifespan is around 10 days (Ravenscroft, 1992). Eggs are approximately 0.5-0.6mm in size and hatch after 10-15 days. Larvae leave characteristic feeding damage above and below shelters made of rolled leaf blades secured with silk, and moult through five instars before overwintering in hibernacula of two or more leaf blades connected with silk. In March or April, larvae emerge from hibernation, construct a tent-like structure from several grass blades, and pupate for 4-6 weeks, held in place by a silk girdle and pad (Ravenscroft, 1992; Ravenscroft and Warren 1996; Moore, 2004; Eeles, 2019). Ravenscroft (1992) explains how *C. palaemon* is found in "open woodland, usually dominated by [sessile] oak *Quercus petraea* or [downy] birch *Betula pubescens*, on gently sloping hillsides, often by the sides of lochs, in sheltered clearings." Eeles (2019) describes wayleaves at Glasdrum NNR in Scotland as prime habitat. He notes it can also be found in wet meadows and at the edge of woodland in areas of scrub. The species is known to occupy a variety of herb-rich biotopes such as scrubby heathland, limestone fenland, and calcareous grasslands throughout its range (e.g. Collier, 1978, 1986; Bretherton, 1981; Warren, 1991; Bink, 1992; Ravenscroft, 1994a). Warren (1990) notes a requirement for high humidity in northern Europe, and a habitat in transient seral stages reliant on periodic management, rather than stable plagioclimaxes.

## 6.2 Methods

### 6.2.1 Habitat Description

Fineshade Wood is situated on the crest of a hill between two valleys: Fineshade Brook to the northwest and Willow Brook to the south (Figure 6.2). The reintroduction site is 80-96m above sea level and occurs on slowly permeable, seasonally wet, slightly acidic but base-rich loamy and clay soil (Handley, 2014; 2019b). Native broadleaves of even-age such as pedunculate oak *Q. robur*, silver birch *B. pendula*, goat willow *S. caprea*, grey willow *S. cinerea*, hazel *Corylus avellana*, elder *Sambucus nigra*, blackthorn *Prunus spinosa*, midland hawthorn *Crataegus laevigata*, and common hawthorn *Corylus monogyna* form low, closed canopies through much of the site. A wetter northeastern compartment is a mixture of high forest conifers and broadleaves. Ride sections are between 15-25m wide and comprised of annually mown central turf zones bordered on one or both sides by ditches with rotationally managed scrub zones extending to the woodland edge.

**Figure 6.3**: A typical ride section at Fineshade Wood, with a central annually mown turf zone bordered by two rotationally managed scrub zones that extend to the woodland edge.

The site is poorly drained, which favours tufted hairgrass *Deschampsia cespitosa*. Annually mown short turf zones are characterised by trampled grass tramlines created through light recreational use. Wood small-reed *Calamagrostis epigejos* is dominant and *A. reptans* abundant where found. Other plant species present include *C. palustre*, rough-stalked meadow-grass *Poa trivialis*, meadowsweet *Filipendula ulmaria*, Yorkshire fog *Holcus lanatus*, soft rush *J. effusus*, hard rush *J. inflexus*, false brome *Brachypodium sylvaticum*, sweet vernal-grass *Anthoxanthum odoratum*, bush vetch *Vicia sepium,* bramble *Rubus fruticosus* agg., meadow foxtail *Alopecurus pratensis*, creeping buttercup *Ranunculus repens*, cuckooflower *Cardamine pratensis*, germander speedwell *Veronica chamaedrys*, cock's-foot *Dactylis glomerata*, creeping cinquefoil *Potentilla repens*, creeping bent *Agrostis stolonifera*, meadow vetchling *Lathyrus pratensis*, and field forget-me-not *Myosotis arvensis* during *C. palaemon* flight periods.

Scrub zones are occasionally bordered by young field maple *Acer campestre*, ash *Fraxinus excelsior*, and *C. avellana* on ditch edges, which are mulched during rotational management. Primary hostplant *B. sylvaticum* is more shade-tolerant than *C. epigejos* and usually found at woodland and ditch edges and on bare ground patches created by mechanical disturbance. *H. non-scripta* is abundant on one ride section only. Rides are sunny, open, and sheltered, although east-west sections are more exposed to wind. A hardcore track borders the reintroduction site with scrubbier vegetation on either side (Figure 6.3). Floristic diversity is higher on the track than on inner woodland rides, which are dominated by grasses. White clover *Trifolium repens*, red clover *T. pratense*, silverweed *Potentilla anserina*, pineappleweed *Matricaria discoidea*, and *L. pratensis* grow in the transition between the track and grassy rides. A more detailed description of the vegetation of Fineshade Wood can be found in Handley (2014; 2019b).

**Figure 6.4**: The hardcore perimeter track at Fineshade Wood.

## 6.2.2 Nectar Plant Sampling

For nectar plant sampling, rides were numbered and split into sections if they intersected other rides (e.g. 1A, 1B, 2A, 2B). A timed walk of the short turf zone (centre) and scrub zone (edge) of each ride section was carried out, and the number of *A. reptans* spikes (whole plants) present in each zone tallied to determine abundance. Both sides of the scrub zone were sampled in one pass using a zigzag walking pattern. Total effort in minutes and the gross tally of *A. reptans* was used to generate an encounter rate for each ride section's short turf and scrub zones. This value – a measure of spike density – accounted for the differing lengths of ride sections (minimum 160m, maximum 520m). Adult *C. palaemon* encounter rates were generated using total volunteer survey effort in minutes per ride section divided by the total number of adult *C. palaemon* recorded per ride section. The following per ride section variables were then inputted into SPSS (IBM Corp., 2021) and tested for association using Spearman correlation: *C. palaemon* abundance (male and female), *C. palaemon* abundance (female), *C. palaemon* abundance (male), *C. palaemon* encounter rate (both sexes), *C. palaemon* encounter rate (male), *C. palaemon* encounter rate (female), *A. reptans* abundance (turf and scrub), *A. reptans* abundance (turf), *A. reptans* abundance (scrub), *A. reptans* density (turf and scrub) *A. reptans* density (turf), and *A. reptans* density (scrub). Data were analysed per year and also for all years combined.

For the 96 tests of association between *C. palaemon* and *A. reptans* variables, using a ρ-value of <0.05 as a baseline, there was a probability that 5%, or 4.8 of our 96 tests would be statistically significant by chance. We were prepared to reject $H_a$ (that *C. palaemon* presence and absence could be predicted by *A. reptans* presence and absence) if the number of statistically significant correlation coefficients did not exceed the number that could have occurred purely by chance. Time of day of adult *C. palaemon* sightings written on timed count forms and attached to casual records was used to review diurnal activity. After 2019-21 records had been entered onto a worksheet, sighting time of day was tallied per hour per sex to generate a summary of active hours at Fineshade Wood. All plots were created in Microsoft Excel (Microsoft Corporation, 2021). Whilst systematic data were not collected on adult *C. palaemon* roosting preference, feeding, and use of ride features such as tramlines (paths of trampled grass in short turf zones created through light recreational use), observations made in the field during 2019-21 flight periods are considered in the Discussion.

## 6.3 Results

### 6.3.1 *C. palaemon* and *A. reptans*

For the 96 tests of association between *C. palaemon* and *A. reptans* variables for individual years and 2019-21 combined using Spearman correlation, 18 (18.8%) were found to be statistically significant – 16 reported a level of significance (ρ-value) of <0.05 (less than 5% probability of chance occurrence), and two <0.01 (less than 1% probability of chance occurrence). Significant strong and moderate positive coefficients were found with eights tests each, and weak coefficients with a further two tests. In 2019, *C. palaemon* male and female abundance was found to be significantly correlated with *A. reptans* density in the scrub zone of ride sections ($r$=0.578, ρ=0.049) (Table 6.1), suggesting that, the more frequent spikes were in the scrub zone, the more often *C. palaemon* of both sexes were encountered.

The same relationship was also found in 2020 ($r$=0.628, ρ=0.012), along with nine other positive coefficients (seven strong and two moderate) between *C. palaemon* and both *A. reptans* abundance and density in both turf and scrub zones. However, tests only indicated statistically significant coefficients between *A. reptans* variables and female *C. palaemon* and both sexes combined – not males independently. In 2021, significant *r*-values were once again found between *A. reptans* and female *C. palaemon* and both sexes combined, but not males (one strong and three moderate). When 2019, 2020, and 2021 data were combined, significant ρ-values but weak positive $r$-values were found between *A. reptans* abundance and both sexes in the scrub zone of ride sections ($r$=0.313, ρ=0.044), and female *C. palaemon* encounter rate and *A. reptans* abundance in both turf and scrub zones combined ($r$=0.310, ρ=0.046) (Figure 6.4).

**Table 6.1**: ♂ and ♀ *C. palaemon* and bugle *A. reptans* Spearman correlation coefficients for A) 2019, B) 2020, C), 2021, and D) 2019-21 combined (Cp=*C. palaemon*, *n*=abundance, *d*=density, *er*=encounter rate, t+f=turf and scrub combined, ***ρ=<0.001, **ρ=<0.01, *ρ=<0.05).

**A**

| | ♂♀ Cp *n* | ♀ Cp *n* | ♂♀ Cp *er* | ♀ Cp *er* | Bugle *n* turf | Bugle *n* scrub | Bugle *n* t+f | Bugle *d* turf | Bugle *d* scrub | Bugle *d* t+f |
|---|---|---|---|---|---|---|---|---|---|---|
| ♂♀ Cp *n* | | 0.644$^{*}$ | 0.921$^{***}$ | 0.468 | 0.098 | 0.430 | 0.263 | 0.084 | 0.449 | 0.151 |
| ♀ Cp *n* | 0.644$^{*}$ | | 0.648$^{*}$ | 0.936$^{***}$ | 0.030 | 0.264 | -0.012 | -0.048 | 0.218 | -0.186 |
| ♂♀ Cp *er* | 0.921$^{***}$ | 0.648$^{*}$ | | 0.560 | 0.200 | 0.493 | 0.277 | 0.200 | 0.578$^{*}$ | 0.200 |
| ♀ Cp *er* | 0.468 | 0.936$^{**}$ | 0.560 | | -0.054 | 0.233 | -0.139 | -0.114 | 0.219 | -0.265 |

**B**

| | ♂♀ Cp *n* | ♀ Cp *n* | ♂♀ Cp *er* | ♀ Cp *er* | Bugle *n* turf | Bugle *n* scrub | Bugle *n* t+f | Bugle *d* turf | Bugle *d* scrub | Bugle *d* t+f |
|---|---|---|---|---|---|---|---|---|---|---|
| ♂♀ Cp *n* | | 0.175 | 0.829$^{***}$ | 0.242 | 0.430 | 0.665$^{**}$ | 0.476 | 0.361 | 0.628$^{*}$ | 0.641$^{*}$ |
| ♀ Cp *n* | 0.175 | | 0.034 | 0.917$^{***}$ | 0.606$^{*}$ | 0.408 | 0.662$^{**}$ | 0.419 | 0.390 | 0.475 |
| ♂♀ Cp *er* | 0.829$^{***}$ | 0.034 | | 0.221 | 0.200 | 0.604$^{*}$ | 0.289 | 0.286 | 0.586$^{*}$ | 0.579$^{*}$ |
| ♀ Cp *er* | 0.242 | 0.917$^{***}$ | 0.221 | | 0.495 | 0.542$^{*}$ | 0.618$^{*}$ | 0.347 | 0.550$^{*}$ | 0.559$^{*}$ |

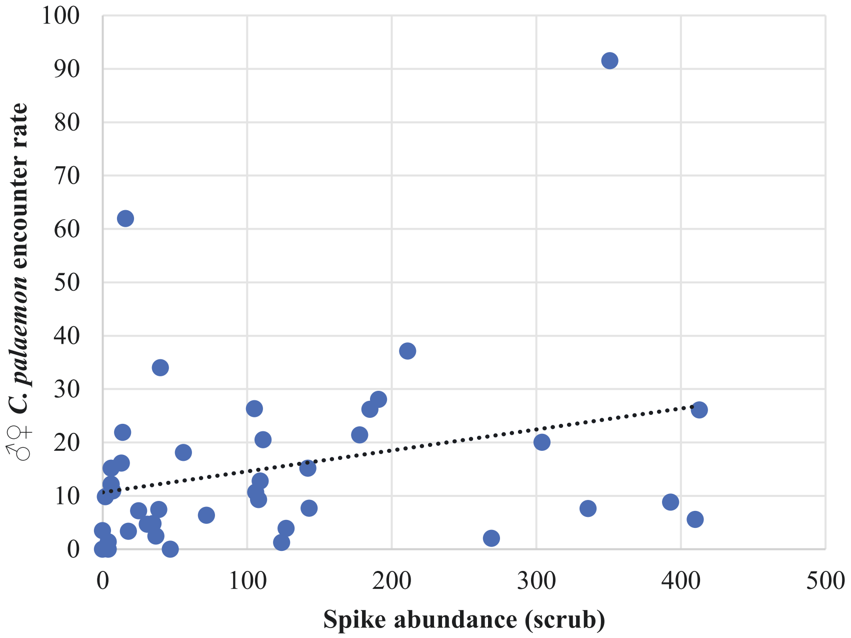
**C**

| | ♂♀ Cp *n* | ♀ Cp *n* | ♂♀ Cp *er* | ♀ Cp *er* | Bugle *n* turf | Bugle *n* scrub | Bugle *n* t+f | Bugle *d* turf | Bugle *d* scrub | Bugle *d* t+f |
|---|---|---|---|---|---|---|---|---|---|---|
| ♂♀ Cp *n* | | 0.549$^{*}$ | 0.970$^{***}$ | 0.531$^{*}$ | 0.613$^{*}$ | 0.161 | 0.494 | 0.494 | 0.142 | 0.381 |
| ♀ Cp *n* | 0.549$^{*}$ | | 0.417 | 0.982$^{***}$ | 0.593$^{*}$ | 0.079 | 0.497 | 0.538$^{*}$ | 0.013 | 0.505 |
| ♂♀ Cp *er* | 0.970$^{***}$ | 0.417 | | 0.416 | 0.506 | 0.138 | 0.419 | 0.427 | 0.115 | 0.326 |
| ♀ Cp *er* | 0.531$^{*}$ | 0.982$^{***}$ | 0.416 | | 0.531$^{*}$ | 0.036 | 0.423 | 0.491 | -0.023 | 0.470 |

**D**

| | ♂♀ Cp *n* | ♀ Cp *n* | ♂♀ Cp *er* | ♀ Cp *er* | Bugle *n* turf | Bugle *n* scrub | Bugle *n* t+f | Bugle *d* turf | Bugle *d* scrub | Bugle *d* t+f |
|---|---|---|---|---|---|---|---|---|---|---|
| ♂♀ Cp *n* | | 0.580$^{***}$ | 0.828$^{***}$ | 0.470$^{**}$ | 0.209 | 0.241 | 0.213 | 0.126 | 0.187 | 0.163 |
| ♀ Cp *n* | 0.580$^{***}$ | | 0.480$^{***}$ | 0.925$^{***}$ | 0.278 | 0.160 | 0.274 | 0.158 | 0.070 | 0.160 |
| ♂♀ Cp *er* | 0.828$^{***}$ | 0.480$^{***}$ | | 0.538$^{***}$ | 0.246 | 0.313$^{*}$ | 0.258 | 0.144 | 0.263 | 0.194 |
| ♀ Cp *er* | 0.470$^{**}$ | 0.925$^{***}$ | 0.538$^{***}$ | | 0.292 | 0.246 | 0.310$^{*}$ | 0.140 | 0.162 | 0.176 |

**A**



**B**

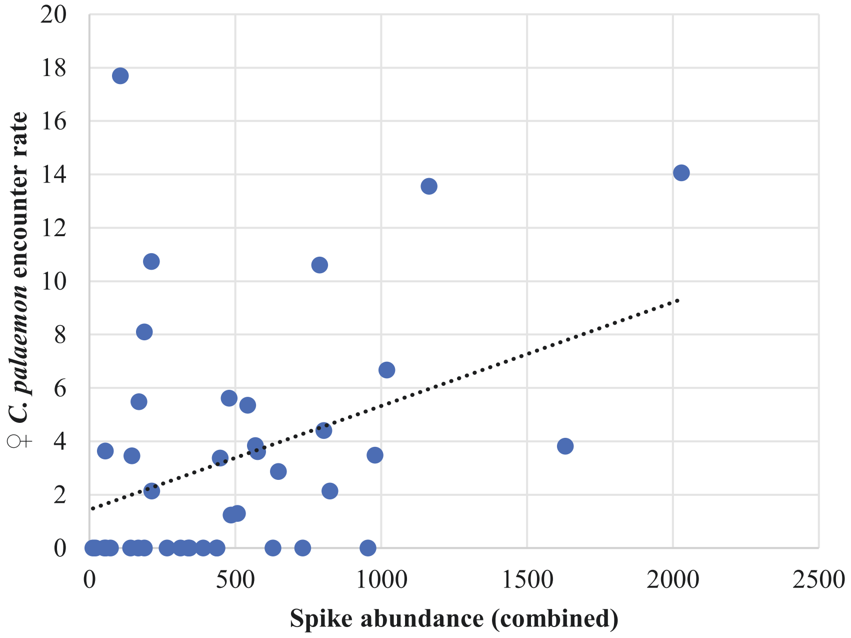


**Figure 6.5**: A) 2019-21 ♂ and ♀ *C. palaemon* encounter rate and bugle *A. reptans* scrub zone spike abundance (*r*=0.310, ρ=0.046), and B) ♀ *C. palaemon* encounter rate and *A. reptans* combined scrub and turf zone spike abundance (*r*=0.310, ρ=0.046) (note differences in x and y-axis value titles and scaling).

No statistically significant relationships were found between *A. reptans* and male *C. palaemon* abundance or encounter rate in either 2019, 2020, or 2021 or when 2019-21 data were combined. A 95% confidence interval of ρ=<0.05 indicates a one in 20, or 5% probability of a statistically significant coefficient occurring by chance. Our tests produced 18 significant *r*-values from 96 tests. At ρ=<0.05, 13.7%, or 13.2 tests could not have occurred purely by chance. True probability was lower still given two tests reported a level of significance of ρ=<0.01 (less than one in 100). Although the risk of a type I (false positive) or type II (false negative) errors was present (McKillup, 2005), there was sufficient evidence of a relationship to accept $H_a$ for female *C. palaemon*.

When 2019-21 *A. reptans* scrub zone abundance was plotted against female *C. palaemon* abundance, female abundance peaked on 1C where *A. reptans* was most abundant (Figure 6.5). Along with 1D to its east and 1B to its west, 1C was one of the most exposed ride sections in the wood. Average wind speeds were typically faster than on surrounding rides due to its width (20-25m), openness, linearity, and largely unobstructed 1378m total length (A-E). Female abundance was also found to be high on 3A and 3B (which formed a cross-ride with 1C), however presence could not be explained by high *A. reptans* scrub zone abundance in either ride section. 15.6% of all *C. palaemon* sightings were made on 3A and 3B in 2019 (22 spikes), 21.6% in 2020 (376 spikes), and 20.0% in 2021 (42 spikes). When outputs were interpreted in terms of turf and scrub zone spike density and female encounter rate instead of gross abundance, the high index for females versus low spike density on 3B in both turf and scrub zones emphasised the disparity between female occurrence and *A. reptans* availability (Figure 6.6).

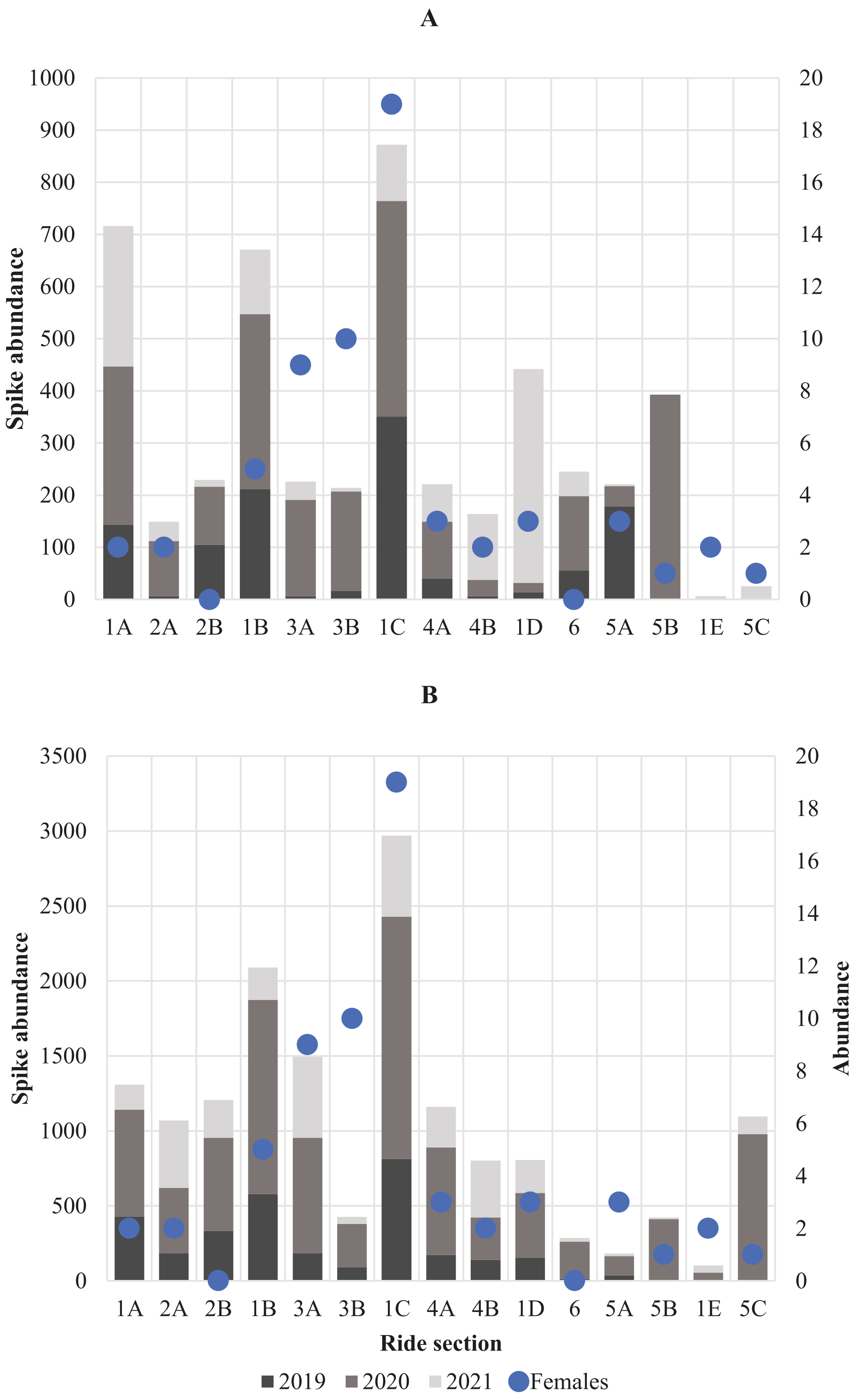


**Figure 6.6**: Bugle *Ajuga reptans* A) scrub zone and B) turf zone spike abundance per year, and 2019-21 combined ♀ *C. palaemon* abundance per ride section (note difference in y-axis scaling). *A. reptans* spike abundance is on the left-hand y-axis and ♀ *C. palaemon* abundance is on the right-hand y-axis. Ride sections on the x-axis are arranged with most westerly on the left and most easterly on the right.

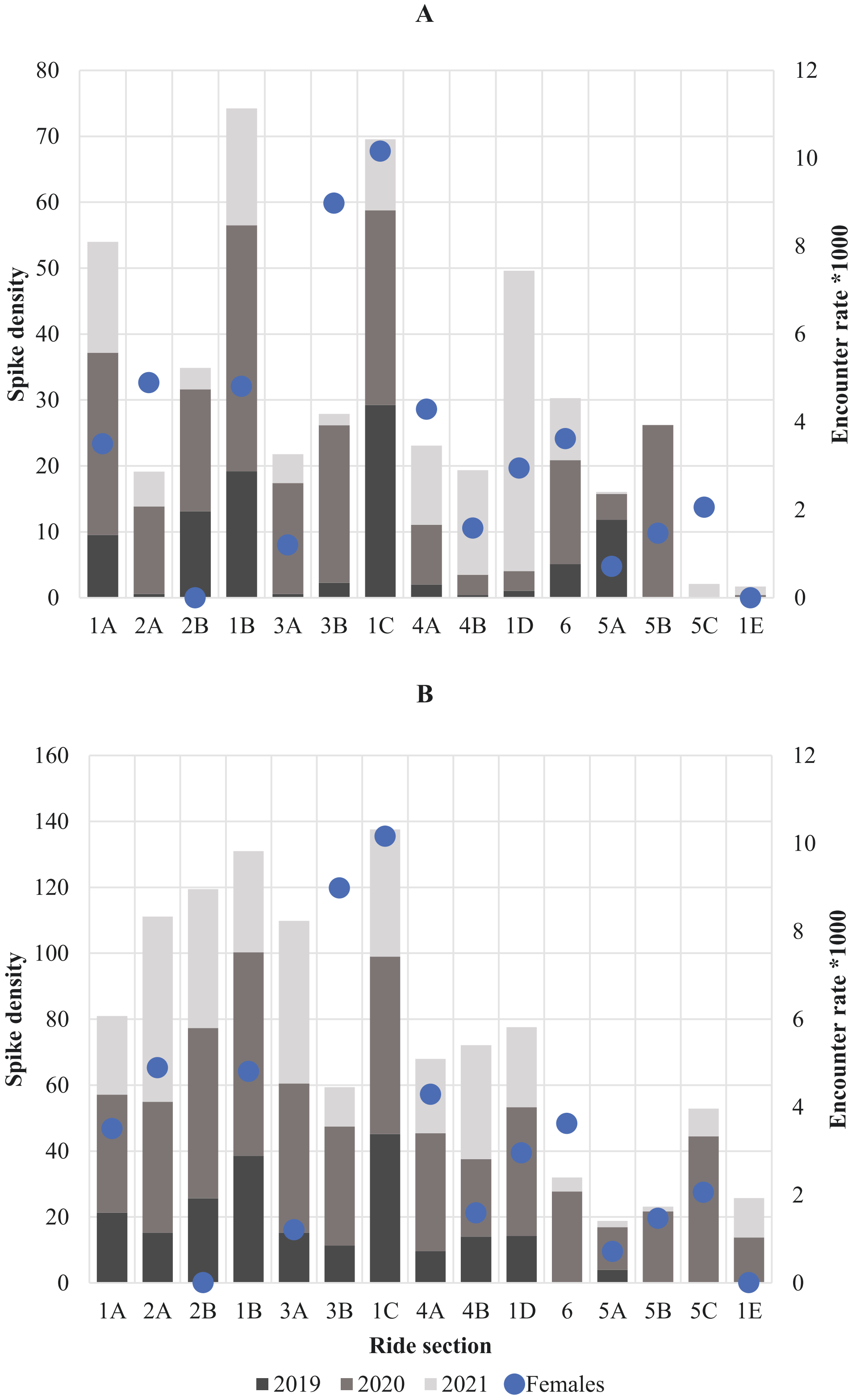


**Figure 6.7**: Bugle *Ajuga reptans* A) scrub zone and B) turf zone density, and 2019-21 mean ♀ *C. palaemon* encounter rate per ride section (note difference in y-axis scaling). *A. reptans* spike density is on the left-hand y-axis and ♀ *C. palaemon* encounter rate is on the right-hand y-axis. Ride sections on the x-axis are arranged with most westerly on the left and most easterly on the right.

## 6.3.2 Diurnal Activity

Sightings at Fineshade Wood in 2019-21 showed females were active from 0818-1825hrs, and males from 0851-1715hrs. Females were most visible between 1200-1300hrs, which is earlier in the day than at Ariundle in Scotland, where females were most often seen between 1500-1600hrs (Ravenscroft, 1992) (Figure 6.7). Male observations at Ariundle peaked between 1400-1500hrs, whereas male observations at Fineshade peaked between 1200-1300hrs – the same hour as for females. Including butterflies of unknown sex, total observations peaked between 1100-1300hrs with 61 per hour – earlier than the 1400-1600hrs peak recorded at Ariundle (Ravenscroft, 1992).

Females at Fineshade were visible from late morning to late afternoon, typically between 1100-1600hrs, however on good weather days activity continued beyond 1700hrs. Female sightings remained consistent between 1300-1500hrs after peaking just after midday. Male observations declined from 38 to 26 between 1300-1400hrs before climbing to 31 between 1400-1500hrs. Females continued to be visible later in the afternoon than males (a total of 31.8% of sightings were female and 68.2% were male between 1500-1600hrs compared to 25.5% female and 74.5% male between 1200-1300hrs). Ravenscroft (1992) observed a higher percentage of activity between 1600-1700hrs (approximately 14% of both total male observations and total female observations) compared to Fineshade from 2019-21 (1.7% of total male observations and 4.9% of total female observations). All unknown sex *C. palaemon* were observed during timed count hours (1000-16000hrs), and abundance peaked between 1000-1100hrs with 16.

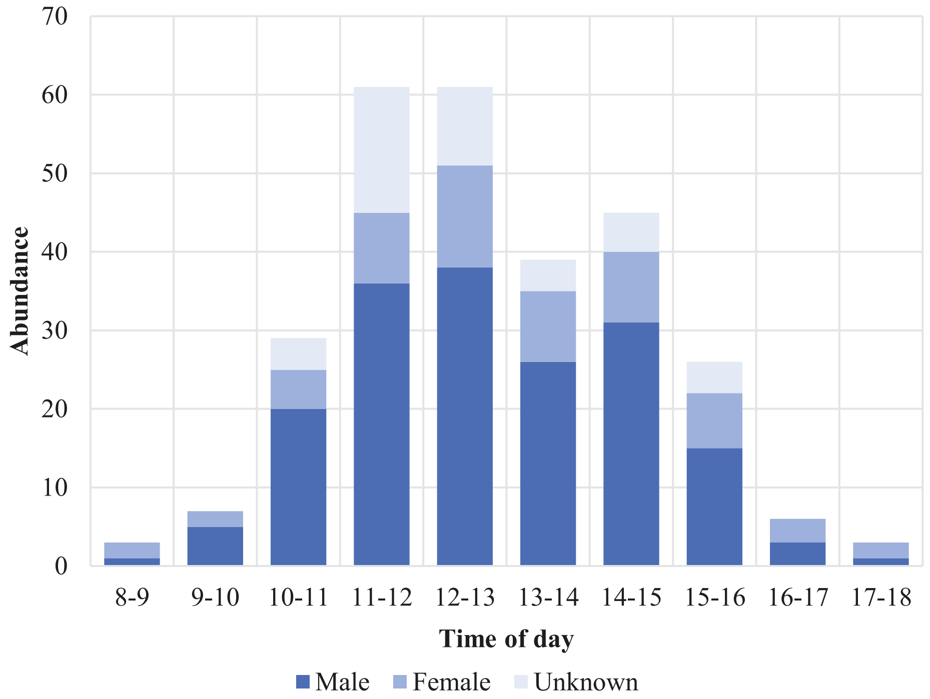


**Figure 6.8**: Diurnal activity of *C. palaemon* at Fineshade Wood, 2019-21 (176 ♂, 61 ♀, and 43 unknown sex).

## 6.4 Discussion

### 6.4.1 The Relationship Between *C. palaemon* and *A. reptans*

*A. reptans* was more abundant in the scrub zone in 2020 (2,380 spikes total) than either 2019 (1,132 spikes) or 2021 (1,282 spikes). The technique chosen for nectar sampling was developed and trialled late in the 2019 flight period when *A. reptans* was beginning to go over, making spikes harder to identify amongst the surrounding vegetation. Owing to its experimental nature, three ride sections (5B, 1E, and 5C) of 15 at the reintroduction site were not sampled in 2019. Surveys were carried out earlier in 2020 and 2021 when spikes were in better condition.

The 2021 season was delayed by a cold spring and series of late frosts. Regrowth on recently managed areas across Rockingham Forest was slower than usual (S. O'Riordan, personal communication). The only year in which ride sections were sampled in representative conditions was, therefore, 2020. Scrub zones rotationally managed during the winter of 2020-21 did not recover in time for the late-May emergence of *C. palaemon* due to the poor weather. Many *A. reptans* spikes growing on unmanaged zones were stunted and showed evidence of frost damage. This combination of factors may explain the decrease in *A. reptans* abundance during 2021 sampling, although some scrub zones (e.g. those on 1A, 4B, and 1D) in second year regrowth responded well to management despite the slow season.

The lack of nectar in scrub zones on most ride sections in 2021 may explain why significant, strong positive coefficients between *C. palaemon* abundance and encounter rates and *A. reptans* abundance and density – found with a combination of scrub and turf zone variables in 2020 – were found only with turf zone variables in 2021. Although *A. reptans* abundance also declined in turf zones in 2021, it was still present in large quantities compared to the number of spikes growing in scrub zones. On four sections of ride one (A, B, C, and D) oriented east-west in a straight line through the centre of the reintroduction site, 911 spikes were tallied in scrub zones, compared to 371 spikes in scrub zones on the other 11 ride sections combined – eight of which are oriented north-south and of comparable length.

The single significant correlation arising from 2019 tests (*C. palaemon* male and female abundance with *A. reptans* scrub zone density) may be due to the smaller ride length and area occupied by the population following the concentrated release of Belgian founder *C. palaemon* in two nets in 2018, which artifically biased the butterflies to specific compartments of the wood, influencing results. As the population dispersed and occupied area and ride length increased, *C. palaemon* was able to reach nectar-rich patches and congregate in these areas in greater numbers, leading to larger quantities of statistically signficant correlations between the butterfly and its favoured nectar plant. By 2021, occupied site area had increased from 65ha to 86ha, and occupied ride length from 4.4km to 5.1km.

A majority of the significant correlations with *A. reptans* are exclusively with female *C. palaemon* data. Female encounter rate is only correlated with one *A. reptans* turf zone variable (abundance) in 2021, and one combined turf and scrub zone variable (abundance) when 2019-21 data are combined. In all other cases, female encounter rate correlations are with scrub zone *A. reptans* density and abundance. Significant correlations between *C. palaemon* encounter rates of sexes combined and *A. reptans* variables can be explained by the inherent statistical strength of the relationship between female *C. palaemon* and *A. reptans*, rather than any statistically significant relationship between *A. reptans* abundance and/or density and male *C. palaemon*. This is emphasised by the lack of relationships between male *C. palaemon* variables and *A. reptans* density and abundance when 2019-21 data are combined. A strong relationship between female *C. palaemon* and *A. reptans* in both scrub and turf zones was present in 2020, indicating that females favour areas where *A. reptans* is either found at higher densities or regularly encountered throughout a zone. Either configuration allows nectaring after short flights, which is an established trait of the species (Ravenscroft, 1992, 1994a).

As we have explained, female *C. palaemon* encounter rate and abundance is correlated with some *A. reptans* turf zone abundance variables. The unknown influence on female abundance on 3A is partially explained by plotting female abundance against turf zone spike abundance instead of scrub zone spike abundance. After doing so, *A. reptans* abundance in the turf zone increases to meet female abundance, indicating that *A. reptans* found in both scrub and turf zones of 1C may be important to females, but only *A. reptans* in the turf zone of 3A influences female abundance. Furthermore, 3A is notable for its abundant *P. aquilinum* and few coniferous Scots pine *Pinus sylvestris* which create shaded conditions unsuitable for *A. reptans*. Spikes are therefore concentrated elsewhere on the ride section. Female *C. palaemon* abundance on 3B (the southern side of the 1-3 cross-ride) cannot be explained by *A. reptans* abundance in either the scrub or turf zone, however.

The high index for female *C. palaemon* versus low spike density on 3B suggests the ride section is functionally different – that it perhaps offers habitat more suited to oviposition, basking, or roosting than surrounding zones whilst still being close to abundant nectar resources. 3B is warmer, more sheltered, and narrower than many parts of the site. It has a southerly aspect (like others on the southern side of the reintroduction site that descend towards Willow Brook), a higher, more open western canopy, and lacks ditches – a characteristic of many rides. The more shaded, wider 2B approximately 220m to its west reported no female sightings throughout 2019-21 (even following the release of Belgian females on the northern end of the ride section in 2019). This suggests that, although 2B *A. reptans* turf zone density is high (comparable to neighbouring ride sections), its cooler, more shaded situation created by overhanging trees, closed canopy, and greater width render it unsuitable for nectaring, oviposition, and other female behaviours.

East-west oriented 1B and 1C are especially wide, with low surrounding canopies. Their northern scrub zones see sunshine throughout the day, and both *A. reptans* and hostplant *C. epigejos* are abundant. These ride sections may, therefore, facilitate a range of female behaviours. Female abundance and encounter rates were higher in the west of Fineshade Wood where *A. reptans* spikes were present in higher densities in turf zones during each flight period. Scrub zone spike density on north-south oriented ride sections west of 4A-4B was poor in 2021 owing to slow post-management regrowth after the cool spring and late frosts. Female encounter rates were again higher in the central 3A-3B-1C area that year, further indicating the area's importance to females. The southern scrub zone of 1C was covered by a dense mat of *C. epigejos* between 2019-21, and the only zone where management was not required owing to a lack of successional growth.

## 6.4.2 Other Feeding Observations

After *A. reptans* had mostly gone over and nectar resources grown scarcer, *C. palaemon* expressed a preference for *R. fruticosus* agg. late in flight periods. At 1428hrs, a female was detected in ranker, unmanaged vegetation bordering the hardcore perimeter track to the southwest of the reintroduction site. The area is considered to be the warmest part of the wood late in the day (A. Wyldes, personal communication). After basking on the track, the female flew into deep, sheltered scrub down a narrow bank. Between 1428-1646hrs, she engaged in prolonged periods of basking interspersed with short flights and extended spells of nectaring, principally on *R. fruticosus* agg. (>60 flowers in total) over a total distance of 25m. She outcompeted bumblebees *Bombus* spp. for nectar resources by flicking her wings as they approached flowers she had already landed on. The temperature remained 19-20°C throughout, with periods of sun and bright cloud. At 1646hrs, the female flew out of the scrubby bank into a ditch on the opposite side of the track to nectar on more *R. fruticosus* agg. before basking on the edge of a flower in full sun. Shortly after 1700hrs, she entered into a rapid, direct 3-4m flight towards a dense tussock near the ditch and was lost. Another female was found further east on the track in similar scrubby habitat nectaring on *A. reptans* and inspecting *M. arvensis* and common mouse-ear *Cerastium fontanum*. *C. palaemon* were also observed mud puddling in ditches during exceptionally dry periods and extracting minerals from the track.

## 6.4.3 Diurnal Activity

*C. palaemon* typically became more active after 1000hrs in suitable weather, however this is when timed counts began each day, suggesting observer bias influenced results to some extent (see Figure 6.7). Similarly, timed counts finished at 1600hrs, after which point observations declined. Some personnel monitored the site before and after the official start and end of timed count shifts, and detected active *C. palaemon* as early as 0818hrs and as late as 1825hrs. Ravenscroft (1992) observed a higher percentage of activity between 1600-1700hrs (approximately 14.0% of both total male observations and total female sightings) compared to Fineshade Wood from 2019-21 (1.7% of total male and 4.9% of total female sightings). The slight apparent drop in total butterfly numbers noted by Ravenscroft (1992) in the middle of the day at Ariundle (1300-1400hrs) is replicated at Fineshade Wood, even with the smaller sample size at the reintroduction site (443 observations at Ariundle from 1988-89, versus 280 at Fineshade Wood from 2019-21).

However, the lull at Fineshade Wood coincides with timed count morning and afternoon shift changeovers, which occur at 1300hrs (shifts run from 1000-1300hrs and 1300-1600hrs), and a reduction in survey effort during lunch hours. This, matched with an anecdotal expectation of reduced detectability of adult *C. palaemon* amongst some personnel, likely accounts for the decline in sightings between 1300-1400hrs. Activity increases again between 1400-1500hrs before declining thereafter. On an especially warm, calm, and sunny evening (approximately 21°C), one female was observed basking until 1825hrs before going to roost on an inflorescence of *A. odoratum* in a turf zone (discussed further in 6.4.5 Roosting). *C. palaemon* was historically known to be active in England from around sunrise (Abbot, 1798) and has been seen flying at Fineshade Wood as early as 0818hrs since its reintroduction (motions at roost have been detected earlier still, at 0728hrs). In suitably warm and sunny early morning weather – likely with mild overnight temperatures – the butterfly is likely to take flight soon after full sun has reached its roost. Timings will vary depending on habitat and roosting site selection.

## 6.4.4 Use of Tramlines and Linear Features

Short turf zones were regularly trampled by personnel carrying out time counts during May-June flight periods. Although the reintroduction site is officially private, members of the public and local residents were known to infrequently walk, cycle, or ride horses through habitat. Personnel on timed counts often worked in pairs and focused on opposite sides of ride sections during shifts. This light recreational use often created two or more trampled grass tramlines with a central reservation of less disturbed vegetation between them and longer grasses on either side (see Figure 6.2). Grass blades and inflorescences often overhung tramlines and created vantage points for male *C. palaemon* with good visibility along turf zones in both directions. *C. palaemon* opportunistically basked in tramlines flush with trampled grass in sunny weather, utilising the higher temperatures, heat reflectivity, and shelter afforded by the microhabitat.

Both sexes regularly used tramlines and turf zones as a means of conveyance along rides, often flying within their bounds in a linear fashion instead of utilising the full width of rides in more erratic flight patterns. This suggests an inherent association with linear features that may be key to our understanding of how *C. palaemon* permeates landscapes, given a female in Ariundle was seen flying down a stream >6km from a known site and males recognise landmarks in territories (Ravenscroft, 1992). Similar route learning and spatial memories have been shown in other insects for foraging and navigation (e.g. Tinbergen, 1932; Collett and Land, 1975; Collett, 2003; 2013).

Dover and Fry (2001) found that the behaviour of scarce copper *Heodes virgaureae*, heath fritillary *Mellicta athalia*, and high brown and Niobe fritillaries *Fabriciana adippe* and *F. niobe* butterflies were affected by the presence of a visual link (builder's warning tape) and a physical link (green horticultural windbreak) between habitat patches in Vestby, Norway. A corridor effect was detected, as mean distances travelled along both links were much longer than with the control (a line of wooden stakes 5m apart). Artificial linear features have also been found to elicit an oriented flight response from bumblebees *Bombus* spp. (Cranmer *et al*., 2011). Additionally, Conradt *et al.* (2000, 2001) suggest that meadow brown *Maniola jurtina* recognise and respond to physical features in landscapes and have a perceptual range of between 100-150m, which they use to identify habitat and orient their movements. The decline of *C. palaemon* in England coincides with hedgerow loss due to agricultural intensification (-36% between 1947-85 – see 4.4.2 of Chapter Four). If the corridor and barrier effect true for other butterflies was replicated by historic populations of *C. palaemon*, a decline in linear features such as hedgerows and field margins linking habitat patches may have limited dispersal and gene flow of the species across landscapes.

Two male *C. palaemon* – a native English butterfly and an individual introduced from Belgium in 2019 – were observed lekking within a tramline. The pair battled atop trampled grass, flapped their wings at high frequencies, displaced dead grass stems, clambered on one another, and faced off on opposing sides of short grass blades in an apparent territorial display. The two males separated after one minute, with the Belgian male returning to perch in the area shortly afterwards. Observations across the three flight periods suggest that light recreational use of short turf zones is not detrimental to the species, and could assist with orientation and thermoregulation, as well as facilitate territorial behaviours.

### 6.4.5 Roosting

A male *C. palaemon* was located at 1400hrs in the centre of a turf zone between two trampled grass tramlines, inert on an isolated *A. pratensis* inflorescence. Conditions were 16°C with a light breeze and overcast skies. At 1512hrs a second male was located approximately 15-20m north of the first male in the same central reservation on another *A. pratensis* inflorescence. At 1638hrs a crab spider (Thomisidae family) was detected on the opposite side of the inflorescence to the northern male (Figure 6.8). Weather conditions remained the same throughout the afternoon, and the two males were left in situ at 1738hrs. Heavy rain and strong winds moved through the site overnight. At 1118hrs the following day in 13-14°C damp and overcast conditions, the southern male was relocated on the same *A. pratensis* inflorescence, which was heavy with moisture and almost horizontal. The inert male, now with slightly crumpled wings, was perched on its upper side. The northern male was absent from its former perch, as was the crab spider. It is possible the male was predated, given crab spiders are ambush predators known to prey on a wide variety of insect pollinators including butterflies (Lovell, 1915). A search of the turf surrounding the absent male was conducted, but nothing was found. The southern male was left later in the morning and not relocated. *C. palaemon* were occasionally seen roosting on *C. epigejos* and *A. pratensis* inflorescence in unsuitably cool (<16ºC) and windy weather, or damp conditions with spells of light rain.

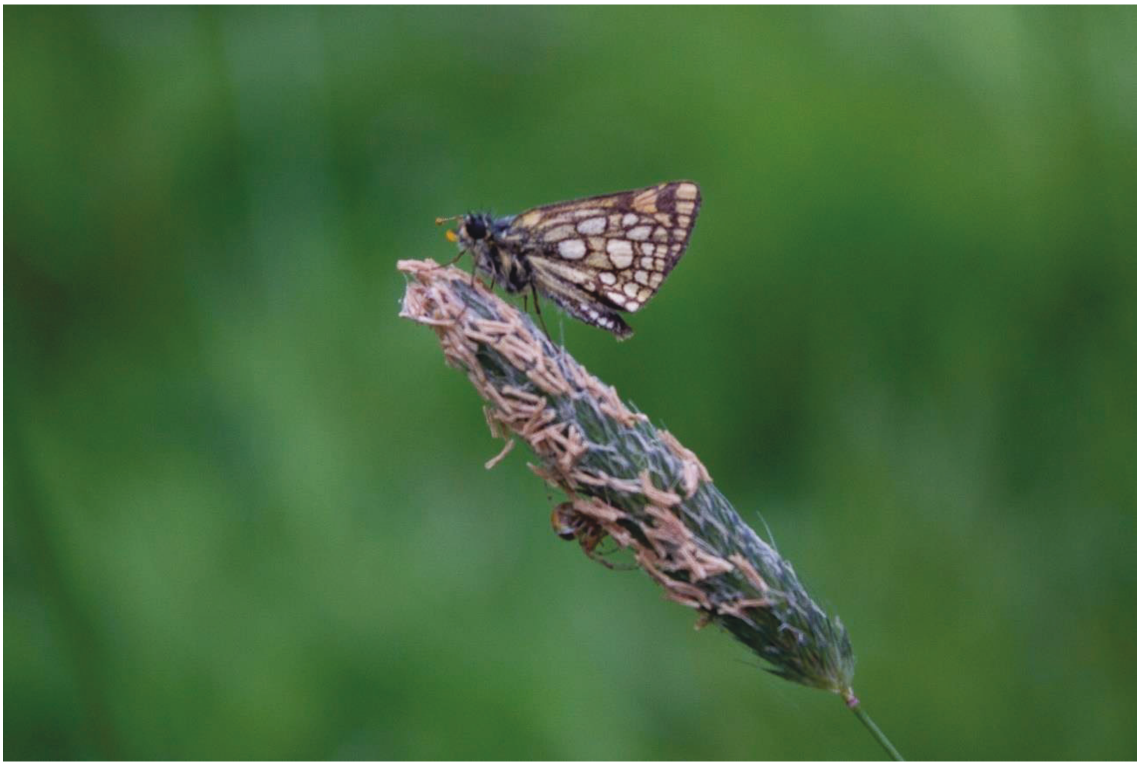


**Figure 6.9**: ♂ *C. palaemon* perched in the middle of a turf zone on meadow foxtail *Alopecurus pratensis* at Fineshade Wood in cool and dull conditions before an overnight storm. Note the crab spider dwelling on the underside of the inflorescence.

A male *C. palaemon* was detected at 1545hrs on *D. glomerata* inflorescence in breezy, cloudy conditions after fluttering in a central reservation between two tramlines. The male remained perched for almost an hour. Thermoregulation decreased over time and the male was not easily disturbed. Passing invertebrates only elicited minor wing twitches or no reaction at all from the butterfly. At 1640hrs, the male reoriented from the northern to the southern side of its perch, then to the west, towards the sun. The base of its wings remained closed, but the tips of its forewings were slightly parted. Shortly afterwards, the male took flight into the centre of the ride section, gaining speed as it did so, before doubling back east over the ditch in an ark above the ranker vegetation. Finally, it ascended in a rapid spiral at the woodland edge beside a mature pedunculate oak *Q. robur*. Visual contact was lost once the male flew above the low, dense silver birch *B. pendula* canopy towards higher treetops.

The male's destination could have been a roost above the surrounding canopy from which it could catch the first of the morning sun. Its erratic flight pattern may have been an escape tactic to evade predators such as birds and dragonflies whilst it gained altitude. The behaviour was not prompted by any obvious stimuli, however butterflies are specially adapted to detect sounds generated by daytime predators (Fournier, 2013) and the male may have manoeuvred in response to a perceived threat. A female *C. palaemon* was also seen to enter into a rapid, unpredictable flight pattern over scrub after being startled by an observer stumbling in a nearby ditch.

A female was detected at 1707hrs basking on a leaf of *R. fruticosus* agg. on a calm, slightly cloudy 22°C evening. The female made short, fluttering flights between *C. epigejos*, *F. ulmaria*, and *D. glomerata* grass blades to bask before nectaring on multiple *A. reptans* spikes at 1814hrs (Figure 6.9). She perched on the western side of a *D. glomerata* inflorescence on the edge of a tramline in a turf zone and closed her wings fully at 1825hrs at a height of 53cm. The roosting site was opposite a gap between two mature *Q. robur* at the wood edge to the east. At 0723hrs the following morning, the female was relocated on the same inflorescence in calm, hazy, humid 17°C weather. She was in partial shade cast by one of the *Q. robur* and became active at 0728hrs, rotating around the inflorescence so that her wings faced the sun, at which time she partially opened them in response to mottled sunlight passing through the *Q. robur*.

The female fully opened her wings at 0800hrs. She proceeded to thermoregulate on the inflorescence before taking flight at 0829hrs in a slow, fluttering fashion to bask on a grass blade of *B. sylvaticum* 3m south of her roost. She grew fidgety at 0849hrs, and curved the terminal section of her abdomen to contact the *B. sylvaticum* leaf before flying approximately 50cm to nectar on a *V. sepium* flower at 0855hrs. She alternatingly basked and nectared after short flights in breezy and light overcast conditions until 1053hrs, when she was lost after a rapid flight towards dense tussocks of *C. epigejos* in the scrub zone. The same female was relocated at 1110hrs basking in a tramline before being lost again at 1123hrs after a series of rapid flights. Her sudden retreat into hostplants in the scrub may have been the period in which she oviposited, given Ravenscroft (1992) has described oviposition flight as fast and direct, interspersed with prolonged bouts of nectaring. The higher ratio of males captured during PMR (see Chapter Five) can be explained by low detectability of females. Females may spend more time nectaring or amongst hostplants in scrubbier vegetation (see 6.4.2), and disperse further from eclosion sites and core habitat where survey effort is highest in search of egg-laying areas (Ravenscroft, 1992). Larger mean distances between captures for females (305.6m) than males (126.3m) at Fineshade Wood support this interpretation.

**Figure 6.10**: ♀ *C. palaemon* at Fineshade Wood after having gone to roost on cock's foot *Dactylis glomerata* on the evening of June 1st 2019.

### 6.4.6 Oviposition and Larvae

No egg-laying was directly observed at Fineshade Wood during 2019-21, partly owing to the site's characteristic ditch structure, which separates many herb-rich turf zones from scrub zones where hostplants are most abundant. Females were often found nectaring in central turf zones, and typically lost once they flew over ditches at pace into scrub. Visibility between zones was often restricted by young trees growing on the scrub side of ditches, meaning that direct line of sight to females was often broken even if no attempt to follow was made. The use of heavy machinery during winter months for mulching work in scrub zones often left behind deep track marks. These hazards – in conjunction with the denser vegetation – created a reluctance to survey for adult *C. palaemon* from within the scrub zone. Personnel instead favoured the more navigable turf zone of each ride section.

In total, six fourth and fifth instar larvae were located during larval searches in autumn 2019, however none were relocated in the weeks following initial detection. Larvae were found exclusively on *C. epigejos* grass blades near or within shelters formed by single grass blades – the edges of which were pulled together with silk threads to form tubular retreats (e.g. Warren, 1991; Ravenscroft, 1995; Moore, 2004; Eeles, 2019). Larvae were found in a variety of microhabitats: the turf zone, near or in ditches, and in deep scrub. Tubes were between 70-109cm high and larvae between 20-27mm in length. The first larva was found on August 31st and the last on October 2nd. Two larvae were measured to be only 130mm apart, resting on different grass blades of the same parent *C. epigejos* plant.

## 6.5 Conclusions

The relationship between *A. reptans* spike density and abundance per ride section and female *C. palaemon* is logical in light of observations made by Ravenscroft (1992) at Ariundle in Scotland. He notes that feeding bouts for females are "generally long" and they "may spend several hours feeding within a small area, only pausing for brief, short flights to new flowers." Females spend larger amounts of time feeding than males, owing to their different energy and reproductive requirements (Ravenscroft, 1994a). Males at Fineshade Wood are not correlated with *A. reptans* density and abundance because they are less selective about flower choice and colour than females (Ravenscroft, 1992). Males were observed defending territories in areas where *A. reptans* patches and hostplants such as *C. epigejos* were present (e.g. 1C), but also habitat dominated by *J. effusus* and bare ground where nectar density and abundance was generally low and *A. reptans* almost entirely absent (e.g. 5A).

Males perch where there are concentrations of females, larvae, or hostplants (Rutowski, 1991; Ravenscroft, 1994a). On many ride sections during the 2019-21 study period, male *C. palaemon* abundance is matched by female abundance. The absence of nectar in Rutowski's description is key and explains why male abundance and encounter rate is not correlated with any *A. reptans* variables. Significant *r*-values between *A. reptans* and variables attributed to both sexes are thought to be due to chance overlaps in male territories or roosting sites and areas where spike density (and therefore female abundance) is higher. Ravenscroft (1994b) notes that the main criterion in territory selection for males is temperature, however temperature is seemingly as important for females nectaring and ovipositing (where shelter may also be a factor in hostplant selection). Targeted vegetation sampling and microhabitat temperature data collection may improve understanding of why female *C. palaemon* express preference for ride sections with both low and high *A. reptans* density and abundance. Studies of other primary, secondary, and tertiary nectar sources at the Fineshade Wood will establish whether they also influence female *C. palaemon* abundance. In particular, *R. fruticosus* agg. once it begins to flower, which is typically late in flight periods.

*C. palaemon* has utilised the inflorescence of at least three grass species growing in short turf zones, unmanaged scrub zones, and overhanging ditches at Fineshade Wood for roosting: *A. odoratum*, *C. epigejos*, and *D. glomerata*. The butterfly is well-camouflaged when roosting due to its small size, brown and cream uns wing colouration, and roosting position, which is always parallel to the inflorescence, granting invisibility to potential predators from at least one direction in calm weather. Individuals detected roosting on grasses at ground-level were never seen positioned on the underside of inflorescences. The instability of such roosts – even in a light breeze – in conjunction with the butterfly's small size make it a difficult moving target for airborne predators when at rest. Selecting the rough and uneven surface of grass inflorescence affords *C. palaemon* good purchase and shelter if confronted by high winds unsuitable for flight. Overnight roosts at ground level not crowded by surrounding vegetation or shaded by woodland are advantageous in good weather, as the butterfly only need expend minimal effort to reorient (if necessary) and open its wings in the direction of the sun to gain temperature whenever conditions are next suitable for flight. The amount of effort required to fly to nectar sources is also reduced from a low-level perch compared to those in trees or elsewhere off-ride (Suarez, 2000).

Our analysis of several aspects of *C. palaemon* ecology at Fineshade Wood suggests it is a hardy, resourceful, and efficient butterfly to which energy preservation is key. *C. palaemon* females prefer short flights and nectaring in concentrated bursts to facilitate behaviours with high energy requirements such as oviposition (Niitepõld, 2019). The species may be capable of spatial memory and route learning to assist with navigation, foraging, and, in the case of males, territorial perching (e.g. Tinbergen, 1932; Collett and Land, 1975; Collett, 2003; 2013). It can also opportunistically roost at ground level where post-dormancy activity has lower initial energy demands. Minimising energy consumption is key when nectar abundance is limited, which can have a negative effect on fecundity, as is the case for some other butterfly species (Boggs and Ross, 1993; Bauerfeind and Fischer, 2005; Geister *et al*., 2008; Lebeau, 2016; Lebeau *et al*., 2018). The short lifespan of *C. palaemon* and its need to maximise activity time and fitness may promote characteristic behaviours such as roosting on grass inflorescence, particularly when nectar availability is low or sporadic, and the association of females with *A. reptans*. Male hesperids lose up to 32% of their abdominal sodium during mating, which they supplement by mud puddling (Warren, 1984; Pivnick and McNeil, 1987). Additionally, male *C. palaemon* spend most of their time guarding territory or basking. Energy preservation through roosting within or near territories may, therefore, be paramount, given that Ravenscroft (1992) hypothesises males are less discerning in flower choice than females because they only feed for energy requirements. To this effect, the roving nature of females implies they are more likely to select roosting sites near nectar sources and hostplants than males.

# 7

# General Discussion: Research Findings, Recommendations, and the Future of the Chequered Skipper Butterfly *Carterocephalus palaemon* in England

## 7.1 Research Summary

Butterfly reintroductions are challenging undertakings that have resulted in species reestablishment in only 24.3% of cases globally (see Chapter Two). Reintroductions in the UK and Ireland have fared better, with a 34.1% success rate for cases with definitive outcomes. The total number of known reintroductions in the UK and Ireland, 394, is 262 more than the rest of the world combined, and 325 more than the whole of Europe. Europe's 40.7% success rate is greater than other regions, however reestablishments on the Continent (22) total only a quarter of those from the UK and Ireland (87). If emergence of *C. palaemon* at Fineshade Wood occurs in 2023, the project can be declared a short-term success, as a resident breeding population will be present in England for the first time in 42 years (1976-2018). Consequently, the number of successful reintroductions in the UK and Ireland can be provisionally raised from 87 to 88.

This is only the second time in history *C. palaemon* has been translocated and reintroduced to habitat within its indigenous range. Project design has relied upon studies of European and Scottish populations due to a paucity of data available from former English populations. The ecological requirements of the species are generally well understood in the UK and western Europe (Ravenscroft, 1992; Moore, 2004), and sites within Rockingham Forest networks are <1km apart – already believed to be within the dispersal range of the species. However, we have proven through PMR at Fineshade Wood that *C. palaemon* is less sedentary than previously thought, and mobile individuals belonging to the reintroduced population are able to travel >1.7km by ride-level measurements (see Chapter Five). We found that five of 30 total *C. palaemon* recaptured through photography from 2019-21 moved >1km from their initial capture points using the same measure. This not only suggests good recolonisation potential of adjacent vacant sites within the Fineshade network, but also indicates how adept historic *C. palaemon* may have been at dispersing across the same sub-landscape.

We demonstrated in Chapter Four that occupied site area and connectivity was an important extirpation buffer in England. Clearance of standards and clearfelling 76.9ha of woodland (of 117.4ha total) between 1950-53 at Castor Hanglands (Collier, 1966) would have created wide, sunny rides. *C. palaemon* abundance accordingly recovered over the following two decades at the reserve. Major steps to widen rides in 1974 after regrowth and insufficient woodland management were too late to save the butterfly (Collier, 1986). The role of wide, managed rides in the provision of good quality habitat cannot, therefore, be overstated. Although more isolated than those within Rockingham Forest networks, large sites such as Skellingthorpe Wood in Lincolnshire (127-year duration of occupation) and Ashton Wold east of the River Nene (117 years) were able to support *C. palaemon* colonies for as long as sufficient good quality habitat remained within site boundaries.

The outstanding question is whether changing land use since the 1900s, lack of agricultural reversion, and loss of fringe habitat since 1977 and the extirpation of *C. palaemon* – all believed to have contributed to its downfall – means landscape permeability is now too low for the reintroduced butterfly to expand its range naturally in Rockingham Forest (e.g. Ravenscroft, 1992; Moore, 2004; Sevilleja, 2021). If this is the case, corridor creation to improve intra-network connectivity must be considered to facilitate dispersal (Figure 7.1). Furthermore, has coppice abandonment and conversion of British woodland to high forest (97% in 2002, up from 21% in 1947) (Hopkins and Kirby, 2007) reduced the likelihood that highly mobile, dispersing *C. palaemon* will be able to locate pockets of good quality managed habitat set within larger unmanaged woodland complexes? Habitat creation through appropriate management such as ride widening, mulching, flailing, coppicing, clearfelling, and clearance of standards will improve connectivity by decreasing the distance between suitable patches at geographically distinct sites.

Assuming increased isolation in England in the 1900s led to increased immobility of successive generations that remained in core habitat – as was the case for the swallowtail *Papilio machaon britannicus* and *P. arion* (Dempster *et al*., 1976; Dempster, 1991) – *C. palaemon* may have formed closed populations in response, limiting emigration potential and gene flow (Ravenscroft, 1992). More mobile individuals may have vacated degrading habitat in search of better quality patches (Thomas, 1985; Warren, 1987: Kuussaari *et al*., 1996; Hanski, 1999). If accelerated decline from the 1940s-50s onwards was a delayed effect of habitat loss and fragmentation of sites that previously supported intermediate colonies, recolonisation potential of the reintroduced colony at Fineshade Wood should not be similarly inhibited.

**Figure 7.1**: Present day view from Fineshade Wood looking east towards Collyweston Great Wood and Bedford Purlieus over agricultural land.

Genetic diversity has been assured through collection of stock from Belgian donor populations that are able to move freely over large, well-connected landscapes. We have shown that larger and less isolated sites – particularly in the north of Rockingham Forest – were buffered against extirpation to a greater extent than smaller, isolated sites elsewhere in England. Given habitat is being restored across Rockingham Forest thanks to ongoing management works, and mobility of photo-recaptured individuals at Fineshade Wood is encouragingly high, we can speculate that a key driver of historic decline and barrier to dispersal is gradually being removed. In conjunction with planned reintroductions to other sites and networks in Rockingham Forest, there is reason to be optimistic about the future of *C. palaemon* in England.

We collated over 3,500 new historic *C. palaemon* records and improved understanding of the species' decline in England (see Chapters Three and Four). The records, when added to existing BNM data, enabled us to establish that site area and connectivity acted as extirpation buffers for the species in Chapter Four. Our research into the history of *C. palaemon* has revealed that the baseline expectation of what is considered normal butterfly abundance has shifted since the 1940s. Bates reported seeing 150 *C. palaemon* and collecting 120 in one day at Wakerley Woods in 1947 with Tozer and Goodson (Bates, *c*. 1945-50), however similar numbers are unthinkable in the present day. Low densities are noted at Scottish and European sites with healthy populations (Warren, 1990; Ravenscroft, 1992). The 2018, 2019 and 2022 Belgian collection trips resulted in the capture of a minimum of 22 and maximum of 50 individuals over two days by large teams (J.P.W., personal observation). The 76% decline in either abundance or occurrence or both of resident and migrant butterfly species in the UK since 1976 reflects the perilous state of wider biodiversity if butterflies are used as an indicator for other invertebrates (Fox *et al.*, 2015). We have proved how entomological diaries, private butterfly collections, and other source of uncollated data can infill historic butterfly distribution and abundance, and draw attention to sites and sub-landscapes that may have previously been overlooked, such as the Luffenham Heath network.

## 7.2 Benefits to Other Taxa

Lepidoptera and other taxa have benefited from targeted management work to improve habitat quality for *C. palaemon* at Fineshade Wood. Woodland clearance to widen rides has created sunny, early-successional, herb-rich habitat in annually mown central zones. Habitat diversity has been improved by rotationally managing scrub zones to allow hostplants such as *C. epigejos* (used by species such as the large skipper *Ochlodes sylvanus* and concolorous moth *Photedes extrema*) to become more abundant (e.g. Stephens, 2005). Young trees and woody plant litter present in scrub zones and on ditch edges provide high, sunny perches for dragonflies elevated above surrounding vegetation. Target species *E. tages* and *P. malvae* – both Section 41 species of principal importance in England under the Natural Environment and Rural Communities (NERC) Act and UK Biodiversity Action Plan (BAP) Priority species – have increased in abundance at Fineshade Wood since 2018.

Woodland habitat supports 39 (66%) of Britain’s butterfly species (Warren and Key, 1991), with 17 of these reliant on woodland in all or part of their range, or have a large proportion of their population associated with woodland (Bulman, 2007). Felling and clearance creates important habitat for woodland specialists such as *L. sinapis* and butterflies associated with open grassland in the wider countryside, such as *H. Lucina*. Bird species associated with woodland edge habitat are also thought to benefit from a net increase in habitat. The nightingale *Luscinia megarhynchos* (Birds of Conservation Concern Red List species -- Stanbury *et al*., 2021) has been heard at the site each year since 2019, as has a second Red List species, the grasshopper warbler *Locustella naevia*. An increase in survey effort at Fineshade Wood since 2018 thanks to Back from the Brink – Roots of Rockingham and Green Recovery Challenge Fund projects has led to an increase in known species. The benefit of management to other taxa is discussed in more detail in Appendix One due to thesis word count limitations that prohibited more detailed analysis.

## 7.3 Stakeholders and Public Engagement

Volunteers generated a total of 660 hours or 88 days of survey effort (equivalent to £13,200 using a rate of pay for skilled volunteers set by the UK government) during 2019-21 flight periods, despite both 2020 and 2021 being pandemic-affected. This demonstrates the collective desire to see projects like the reintroduction of *C. palaemon* succeed. The unique scale of timed count recording by experienced butterfly surveyors and photographers at Fineshade Wood enabled individual *C. palaemon* to be tracked using PMR. We have proven that this novel, non-invasive surrogate for MRR can be used to determine butterfly lifespan, abundance, and mobility, and indicate dispersal range of the species in England.

The strength of support expressed by project partners such as Forestry England (FE) and its role in the success of the reintroduction to this point through effective woodland ride management must also be acknowledged. Most of FE's work was not funded by Butterfly Conservation, and was carried out independently after consultation. FE's ongoing commitment to management will be a deciding factor in the long-term success of the project. Support from other stakeholders across the Rockingham Forest landscape through agro-environment schemes will exert a similar influence on its outcome. A sustained programme of complementary, targeted habitat restoration is essential for the reintroduction of a specialist butterfly like *C. palaemon*.

The species' dependence on sunny, sheltered, deciduous woodland rides with frequent *A. reptans* and *C. epigejos* and its other well-documented ecological requirements would render clandestine releases at unmanaged and unsuitable habitat grossly ineffective (e.g. Farrell, 1973; Collier, 1986; Ravenscroft and Warren, 1992; Moore, 2004). The scale of interest from the general public in the reintroduction, extent of press coverage, and community engagement through surveying, volunteer work parties, and guided walks (first offered in 2022) has demonstrated the appetite for reintroducing extinct butterfly species to England and benefitting other taxa through landscape-scale solutions (e.g. Beament, 2019; Fernandez, 2019; BBC News, 2018, 2019, 2020; Barkham, 2022). The reestablishment of *C. palaemon* in England would be a major success story for conservation, add to the canon of successful Butterfly Conservation projects, and serve as a case study for future evidence-based reintroductions.

## 7.4 Rockingham Forest Reintroduction Summary, 2018-22

Following reintroduction in 2018 and colony reinforcement in 2019, planned reintroductions at new sites in 2020 and 2021 were cancelled as a consequence of mitigating circumstances. The COVID-19 pandemic introduced temporary restrictions on domestic and international travel and also limited the maximum size of gatherings. Only six personnel were officially permitted to access the reintroduction site in 2020 to monitor adult *C. palaemon*. Total survey effort decreased accordingly, down from 10,207 survey minutes in 2019 to 6,263 minutes in 2020. In 2021, no such movement restrictions were in place during the flight period, and many volunteers from 2019 returned to Fineshade Wood. Timed counts were started prematurely in 2021 in unsuitable conditions in response to early emergence the preceding year. Pre-emergence monitoring continued for nearly three weeks before the first adult *C. palaemon* was recorded. Emergence in 2019 followed a late summer drought in 2018, however this had no obvious adverse effect on the population (it must be noted, however, that no baseline good emergence had been established, given this was the first generation in England since 1976). Within a 50m stretch of a single turf zone – the patch itself within 100m of the site of a 2018 release tent – five males exhibiting territorial behaviour were simultaneously under observation on May 21st.

In 2020 and 2021, individuals dispersed more widely from release points and were detected in unmanaged compartments of the woodland complex, as well as sunny, warm patches where rides terminated. Occupied ride length increased year on year, from 4.4km in 2019 to 4.7km in 2020, and 5.1km in 2021. Occupied area also rose, from 65ha in 2019 to 70ha in 2020 and 86ha in 2021. Early details suggest 2022 was good year for *C. palaemon* at Fineshade Wood, with a provisional total of 146 records (a 124.6% increase on 2021). 2022 has been a historic drought year in England, and good emergence in Rockingham Forest in 2023 should quash any lingering speculation that drought meaningfully contributed to the extirpation of *C. palaemon* in England in the 1970s. However, poor emergence may indicate that *C. palaemon* is somewhat vulnerable to drought, necessitating further research into the impact of climate change on the butterfly that builds on the work of Maes *et al.* (2019).

Butterfly Conservation successfully applied for another tranche of funding in 2021 (Green Recovery Challenge Fund), which enabled a further release to take place in Rockingham Forest this year (2022). Sources of funding to extend the project beyond March 2023 have already been identified. The reintroduction is classified as partially successful in a 2020 Natural England summary of reintroductions and translocations in the UK (Wells and Heydon, in press). The report cites strong partnership between state conservation organisations in Belgium and England, universities, environmental non-governmental organisations (NGOs), and land managers amongst its reasons for success. Delays in habitat management work due to wet weather and poor ground conditions, and restrictions caused by COVID-19 were considered major difficulties faced (Bourn *et al.*, in press – see Appendix Five).

## 7.5 Recommendations for Future Reintroductions of *C. palaemon* to England: The Logistics of Collection, Translocation, and Captive Rearing

### 7.5.1 Introduction

The approach to collection, translocation, and release of adult *C. palaemon* in Rockingham Forest developed by Butterfly Conservation in collaboration with the ZSL has proven to be entirely fit for purpose, judging by the success of the project to this point. However, the field of reintroduction biology is still in its relative infancy, and new standards for translocations are regularly being released and revised (e.g. Invertebrate Link, 2010; IUCN, 2013; Daniels *et al.*, 2018; DEFRA, 2021a). Given the low success rate of cases in both the UK and globally as detailed in Chapter Three, it would be unwise to assume that lessons cannot be learnt from new, successful butterfly reintroductions. Refining methodology and the cost-effectiveness of projects will limit the impact of worst-case scenarios in the future.

No single set of guidelines can be a one-size-fits-all for translocations, given that the ecological requirements of invertebrates are species-specific. We must continue to iterate on proven frameworks and refine best practice per species to increase the likelihood of future projects arriving at similarly satisfactory outcomes. Based on observations made during the course of Back from the Brink – Roots of Rockingham and Green Recovery Challenge Fund projects, we offer a set of recommendations specific to *C. palaemon* that build on an establish platform of protocols and reintroduction success in England (Shadbolt and Sainsbury, 2021).

### 7.5.2 Refrigerating Stock

Adult butterflies should be refrigerated immediately following capture to preserve stock condition and prioritise animal welfare in accordance with IUCN (2013) translocation guidelines (5.1.5). Stock should be transferred from nets to transparent specimen pots and labelled as described in Shadbolt and Sainsbury (2021) (Figure 7.2). Pre-release fit for release health examinations must be conducted promptly in cool environments to ensure butterflies are not reactivated before release. Whilst in captivity, ambient storage temperature must be monitored to limit variance. If cooling blocks in cool boxes are used, attention must be paid to stock housed directly next to blocks, as they can become overly chilled compared to those positioned further away from cold sources. Temperature variances of up to 5°C were found between stock stored at the top of storage boxes compared to those stored at the bottom next to cooling blocks during *C. palaemon* translocation in 2022 (6°C-11°C). Refrigeration to 8-10°C is proposed for *C. palaemon* given the butterfly typically activates in sunny weather between 14-16°C.

**Figure 7.2**: Susannah O'Riordan (Butterfly Conservation) transferring an adult *C. palaemon* from a butterfly net to a specimen pot after capture in Belgium, May 2018.

Butterflies cooled to lower temperatures (6°C) took longer to reactivate after being transferred to vegetation in Rockingham Forest. Excessively cooled stock may be at a disadvantage if only a small release window is available due to weather or time of day constraints. A clutch of eggs was found in one container in 2018, indicating that insufficient cooling can lead to distress and activation even in absence of light triggers. Water vapour in specimen pots used to house individual butterflies translocated to Rockingham Forest was observed to condense in lower temperatures. The potential to improve the butterfly's grip on pot walls should also be explored to limit disturbance in the event of storage containers being jarred. A narrow strip of fine sandpaper or other textured material should be affixed to an inner wall of trial pots with glue or other water-resistant adhesive to function as an artificial perch. A strip may prevent captive butterflies from coming into contact with condensation or excessively cold surfaces if utilised. Square pots are recommended as they can be packaged more rigidly than circular pots and are easier to handle securely when damp or contaminated. A high standard of packaging and temperature control will limit stress and enhance post-release performance (IUCN, 2013).

### 7.5.3 Collection

No mortality occurred in adult stock transported in private vehicles from Belgium to England as a result of captivity, refrigeration method, or mode of transport used. All stock captured in Belgium was released in Rockingham Forest within 48 hours between 2018-22. A team of Butterfly Conservation staff liaised with Belgian entomologists in 2018, 2019, and 2022 and travelled in private vehicles to collect stock from donor sites. Several logistical challenges must be overcome in order for trips to be successful. For representatives from England (or any distant or overseas nation) to be involved in collection and translocation of butterflies, trips must be timed to coincide with species emergence and weather conditions suitable for bulk capture in short time periods (two days maximum as established by this reintroduction project).

Hospitality and public transportation must be booked in advance if flexible options are unavailable, and the availability of local collaborators confirmed before departure. This approach has the potential to be inefficient on scheduling and cost grounds. Cost-efficiency is particularly important for smaller invertebrate organisations, conservation charities, and academic institutions with limited labour and financial resources. Last-minute logistical challenges can arise in the event of poor weather or other unanticipated delays, resulting in costly rescheduling or cancellations. Even if trips go according to plan, travelling personnel must remain on site for one or two nights with captive refrigerated stock until quotas have been reached. This unnecessarily extends the time between capture and release of butterflies.

An approach that does not involve personnel travelling to foreign donor sites is recommended. A protocol for capture, storage, and refrigeration of stock should be agreed upon by all project partners. It is proposed that a member of DRM staff be stationed in the donor country in order to carry out pre-translocation health examinations, with a second in the host country, ready to conduct pre-release examinations. A representative of the donor country's collection team should inform the host organisation once conditions are suitable for bulk capture of butterflies. After stock has been placed in storage and health examinations performed, a member of the collection team or other authorised personnel should escort the container(s) to a courier or exchange point in (or bordering) the host country for same-day handover. Stock should be transported to the reintroduction site ready for release the following morning or day to ensure a maximum 24-hour turnaround.

This approach requires a status of readiness and a daisy-chain of dependency that will be satisfactorily met through good communication, strong international collaboration, and a degree of trust between affiliates. It eliminates the need for staff to travel to donor sites and prearrange accommodation, ensures all parties are not required to synchronise availability for stock collection, reduces captivity duration, and does not rely on unreliable long-term weather forecasting for trip scheduling. Local teams can react to emergence peaks without delay to reach quotas quickly due to high population density, and collectors can be more selective when choosing stock for translocation. Collection of fresh *C. palaemon* females carrying full clutches of eggs is key, as females are thought to only mate once (Ravenscroft, 1992). This process can be repeated for as many days as required or is deemed permissible, providing local teams are available to collect stock and assist with translocation. In the case of a delay caused by insufficient quantities of butterflies being collected in one day, overnight refrigeration of stock in either the origin or destination country and 24-hour release postponement would only result in captivity approximately equal to the 48 hours already known to be safe for the species. However, when handling short-lifespan invertebrates such as *C. palaemon* and attempting to establish vulnerable founder populations, methods that reduce captivity time and increase cost-efficiency should be sought and actioned whenever possible.

### 7.5.4 Transport

Hybrid motor vehicles and rail have been used for 2018-22 translocations. Although these are the least environmentally harmful modes of transportation realistically available, they are slow, vulnerable to the impact of traffic congestion, rail delays and cancellations, and high variability of ambient temperatures surrounding storage containers. Conservation organisations must be especially conscious of the environmental impact of collection trips to donor sites and negative public perception surrounding particulate matter emissions. However, this must be delicately weighed against the wider benefits to biodiversity generated by species reintroductions and associated habitat management. Although private planes and helicopters generate more indirect climatic non-$CO^2$ pollutants than other modes of transport (Department for Transport, 2021), they should be considered in exceptional circumstances such as species reintroductions to enhance translocation efficiency.

Providing suitable landing sites can be identified in proximity to both donor and reintroduction sites, aircraft are faster and more direct than ground-based alternatives. The speed at which stock can be translocated using aircraft is particularly useful when dealing with narrow release windows. Air travel costs are high in comparison to motor vehicles and rail, however. If costs cannot be subsidised or waived, the use of aircraft should be questioned when projects are financially constrained. Couriers specialising in hauling biological cargo in temperature-controlled environments (e.g. DHL Freight Coldchain) should be considered as an alternative. A courier can act as a surrogate for personnel nominated to accompany stock to a handover point. Storage container temperature should be monitored throughout translocation using remote thermometers placed between each row of pots. Different cooling block and pot configurations should be trialled in advance of collection to determine which is the most reliable. In ideal circumstances, vaccine carriers or cold chain boxes with programmable internal temperature functions should be used, but these may be cost-prohibitive.

### 7.5.5 Release

Release area suitability at reintroduction sites is dependent on weather conditions and time of day. If adult *C. palaemon* are transferred to vegetation from pots in conditions unsuitable for flight (e.g. early morning <14-16°C), they should be housed within a specialised mesh tent (Figure 7.3). A controlled environment will allow stock to warm up gradually as ambient temperature rises whilst being protected from predation. If release is performed in the evening before sunset (>16°C), stock should be transferred to *A. reptans* spikes or broadleaves close to the ground in direct sunlight. Stock should be spaced out in habitat and the location of each butterfly demarcated to prevent accidental trampling.

If release is carried out in the middle of the day in high ambient temperatures (>20°C) but overcast skies, stock should be transferred to *A. reptans* spikes, high perches such as *C. epigejos*, *D. glomerata*, *A. pratensis*, or *A. odoratum* inflorescence, or other suitable broadleaves. Under sunny skies and in warm temperatures (>16°C), release should take place in shaded, sheltered settings soon after pots are removed from storage. Lids should be removed from pots as soon as possible in case butterflies react to environmental stimuli and reactivate. Stock that remains inert should be transferred to shaded vegetation. Areas where *A. reptans* is abundant should always be favoured, as translocated *C. palaemon* often seek out nectar soon after release.

**Figure 7.3**: Butterfly Conservation staff (left to right: Dan Hoare, Sam Ellis, and Nigel Bourn) erecting a mesh tent to temporarily house translocated Belgian *C. palaemon* at Fineshade Wood in May 2018.

## 7.5.6 Captive Rearing

Captive rearing should be considered using stock from geographically distinct donor populations to ensure sufficient genetic diversity (e.g. Descimon, 1988; Łukasiewicz, 2016). Collection should be prioritised until a captive generation has been successfully reared through to adulthood. Captive rearing acts as insurance against low collection totals, but can also be a complementary technique to increase the quantity of released butterflies even in the case of full quotas being reached. Providing genetic diversity, welfare, and DRM standards are satisfactorily met, captive rearing is potentially a more cost-effective and less environmentally harmful way to reinforce populations than collection trips to donor sites. Experimental trials should be undertaken to determine the viability of this method in advance of it being formally incorporated as a tool to support (or replace) established reintroduction methods. The health of captively-reared stock and disease risks associated with this translocation method should be assessed using DRM and PRHS protocols, and as part of ongoing population sampling efforts post-release (e.g. Nicholls and Pullin, 2000; Davis *et al*., 2020; Shadbolt and Sainsbury, 2021). Low quantities of captively-reared stock (especially unmated females) should not be reintroduced to a site which does not already support a *C. palaemon* colony. Emergence of a captively-reared generation would likely be staggered, not simultaneous, even in a controlled environment (Moore, 2004).

Encounter rates would therefore remain low throughout the flight period at the release site, reducing mate-finding potential and the likelihood of reintroduction success.

### 7.5.7 Habitat Management

At reintroduction sites, good communication with landowners responsible for habitat management is essential. A rotational management scheme was developed for Fineshade Wood in collaboration with Forestry England for the reintroduction of *C. palaemon* and actioned each winter (annually mown turf zones with flailed and mulched scrub zones). Although work was undertaken in accordance with the plan, it was occasionally overzealous and did not preserve margins of hostplant known to have been previously utilised by female *C. palaemon* for oviposition. Slow regrowth in spring 2021 due to cold weather and late frosts resulted in a reduction in *A. reptans* and hostplant abundance in some managed zones. Attention should be paid to the rate of regrowth on rides and management cycles adjusted if necessary to maintain lushness. Areas known to be utilised by *C. palaemon* for specific purposes (e.g. oviposition) should be communicated directly to equipment operators who perform work to ensure small compartments are left undisturbed. The protected status of such areas should be reviewed annually after butterfly abundance data and field observations have been analysed to determine whether they should remain undisturbed or be brought back under management. Plug-planting of *A. reptans* should be considered if spring regrowth is slow and nectar thought likely to be scarce.

Warren (1990, 1991) proposes ride profiles of 3-6m, 5-8m, and 25-35m wide for *C. palaemon*. He notes that *C. palaemon* favours narrow rides through low, regenerating woodland in England and northern Europe. The lack of suntraps, scrapes, glades, and ride sections of varying widths and canopy densities at reintroduction sites should be addressed to create a more diverse habitat matrix (e.g. Stephens, 2005). At present, there is no indication rides >20-25m wide are more beneficial to *C. palaemon* in England than sections up to 10m narrower. The amount of sunlight able to penetrate to ride level is thought to be more important than ride width. Experimental coppicing to open canopies should be trialled as an alternative to deforestation for rides >10-15m wide, chiefly on east-west oriented sections with more shaded southerly turf and scrub zones, in order to benefit woodland butterfly and moth species (Greatorex-Davies and Marrs, 1992; Bulman, 2005; Stephens, 2005).

*A. reptans* spikes were observed to be in better condition for longer periods of time at Fineshade Wood if afforded occasional shade. Targeted coppicing will allow *A. reptans* spikes in turf zones to be periodically shaded but mostly remain in full sun. Retaining soil moisture and microhabitat humidity levels will become more important as heatwaves and droughts become more common due to climate change and desiccation risk increases accordingly (Settele *et al.*, 2008; Maes *et al.*, 2019). Work to improve woodland connectivity and defragment sub-landscapes through the creation of unbroken corridors (e.g. herb-rich field margins, roadside verges, and wildflower patches) in collaboration with adjacent landowners should be considered in order to improve the likelihood of *C. palaemon* recolonisation.

Private sites should be prioritised for reintroductions whenever possible and projects kept confidential until reestablishment according to Red List criteria has been achieved (Fox *et al.*, 2022). Publicity is an important return on investment (ROI) for lead organisations, landowners, and other stakeholders, however confirmation of stable breeding populations must take precedence over ROI. If initial private site reintroduction is not possible due to funding stipulations, unsatisfactory habitat quality, or other factors, public site reintroduction should be accompanied by agreed timescales of confidentiality between stakeholders. This will ensure habitats are protected from excessive disturbance caused by increased public interest in the initial stages of reintroductions when colonies are most vulnerable to extirpation. Limited public access also grants greater freedom to researchers monitoring butterflies and ensures data can be collected in an unhindered fashion and pressure-free environment. Patrolling volunteers could ensure members of the public behave in an appropriate manner during flight periods.

*C. palaemon* is currently only a partially protected species in the wild in the UK, covered by Schedule 5, Section 9, Parts 5(a) and 5(b) of the Wildlife and Countryside Act, which was introduced in 1981, after the butterfly's extirpation from England. Part 5(a) and 5(b) state that, if any person "sells, offers or exposes for sale, or has in his possession or transports for the purpose of sale" or "publishes or causes to be published any advertisement likely to be understood as conveying that he buys or sells, or intends to buy or sell" they shall be guilty of an offence. Schedule 9 is revised every five years. Arguments for greater protection of *C. palaemon* through future inclusion in Schedule 5, Section 9, Part 1, " if any person intentionally kills, injures or takes any wild animal included in Schedule 5, he shall be guilty of an offence" should be made to the UK government now that the butterfly has been reintroduced to England. *C. palaemon* will be eligible for Red List assessment in 2023 as a resident breeding species established in England for five or more years. It is presently considered Nationally Scarce according to a rarity assessment (Fox *et al*., 2022).

## 7.6 Research Recommendations

### 7.6.1 Historic Data

Through this study, we have demonstrated that known records can be increased by collating data from museums specimens, private specimens, published and unpublished texts, and anecdotal evidence. These methods could be replicated for other extinct or endangered invertebrates to determine historic distribution, abundance, and range. This information, collated and analysed in the design phase of projects, would inform reintroduction sub-landscape and site selection and description of optimal habitat for the focal species. Drivers of decline could be outlined with greater confidence and accuracy using larger datasets generated through the collation of historic data, reducing reliance on limited historic evidence-based conclusions to determine the viability of reintroductions and probability of reestablishment. Historic data on *A. crataegi* and other extinct invertebrates should be collated in advance of a reintroduction proposal to ensure historic distribution and decline is thoroughly understood before project design is finalised.

## 7.6.2 Habitat and Population Sampling

PMR is a promising technique for monitoring populations of introduced butterflies, and its advantages have been outlined in Chapter Five. Studies to determine macronutrient concentrations of hostplants have been carried out in Scotland and France (Ravenscroft, 1994a, 1994c; Moore, 2004), and butterfly occurrence probability has been related to Ellenberg Indicator Values (EIVs) for moisture, soil reaction, and nitrogen of vegetation at Dutch Butterfly Monitoring Scheme sites (Oostermeijer and van Swaay, 1998). Similar studies to establish the relationship between hostplant selection, macronutrient concentrations, microhabitat temperature, humidity, and shade levels at known larval sites in England will help to predict presence or absence of larvae, growth, and mortality rates. This could improve encounter rates during larval and adult female searches and indicate prime oviposition patches. The occupant species of vacant larval tubes was unable to be confirmed in situ as *O. sylvanus* larvae – also present at the reintroduction site – construct tubes similar to *C. palaemon*. Environmental DNA (eDNA) metabarcoding of hostplant grass blades with vacant larval tubes should be used to retrospectively confirm occupant species. DNA extraction using forensic swaps or lysis buffer and incubator methods should be trialled in collaboration with a molecular laboratory. This technique is rapidly becoming an established practice in ecology but has not yet been attempted on butterfly species in the field (e.g. Ruppert, 2019; Kudoh *et al.*, 2020; Breton *et al*., 2022).

Temperature and humidity sensors (e.g. iButton thermocrons) and a weather station should be placed at reintroduction sites to create detailed temperature and humidity heatmaps. Weather data can be overlaid with temporospatial adult butterfly data to establish whether presence and absence can be predicted by variations in micro- and macrohabitat temperature and humidity. We have recommended PMR as a non-invasive surrogate for MRR to estimate abundance, track mobility and lifespan of individual butterflies, however development of radio microtransmitters small enough to attach to the thorax of *C. palaemon* would be a novel approach to spatiotemporal data collection from a reintroduced butterfly population in England.

In North America, microtransmitters have been attached to the monarch *Danaus plexippus* to study annual migration of the species to the southern US, Mexico, and Caribbean (Knight *et al*., 2019). Radar transponders weighing 12mg have also been attached to thoraxes of small tortoiseshell *Aglais urticae*, peacock *Aglais io*, red admiral *Vanessa atalanta*, comma *Polygonia c-album*, and painted lady *Vanessa cardui* in Harpenden, Herefordshire to track flight paths in agricultural landscapes using harmonic radar (Cant *et al*., 2005). Similar devices have been used on turnip moths *Agrotis segetum* (Riley *et al*., 1998), honeybees *Apis* spp., and bumblebees *Bombus* spp. to obtain telemetry on space use and flight distances (e.g. Osborne *et al.*, 1999; Capaldi *et al.,* 2000; Riley *et al*., 2003; Hagen *et al.*, 2011). The rate of development of nanotechnology, downsizing of telemetry transmitters for use in other fields (e.g. Wargo Rub, 2020), and proof of concept in North America suggests specialised microtransmitters could be manufactured for use on smaller butterfly species.

Creation of a patch occupancy model to compensate for absence of direct evidence will indicate whether unoccupied sites within sub-landscapes were likely historically occupied. This will benefit Rockingham Forest landowners and project stakeholders by enabling present-day management works to be tailored to incorporate dynamic habitat patches within sub-landscapes**.** Lastly, in Chapter Four we suggested mapping linear features such as hedgerows and field margins in historic landscapes to better understand how corridors facilitated movement of extirpated *C. palaemon* populations in England. Given that the species has been observed flying along streams in Scotland (Ravenscroft, 1992) and tramlines at Fineshade Wood, work could be done to map linear features and classify land use between sites within present-day Rockingham Forest networks in order to produce sub-landscape permeability indices. An experimental release of marked common butterflies of similar mobility to *C. palaemon* could be carried out on the boundary of one geographically distinct site within a Rockingham Forest network next to a linear feature such as a hedgerow (see 6.4.4 of Chapter Six). The boundary of a neighbouring site could then be surveyed to establish how many marked individuals are able to bridge across within a set time period (possibly three weeks based on a typical *C. palaemon* flight period). This butterfly data could then be fed into a permeability index to generate insight into the level of connectivity between sites and likelihood of natural *C. palaemon* recolonisation following release at either site.

## 7.7 Closing Remarks

Back from the Brink – Roots of Rockingham resulted in the return of *C. palaemon* to England after an absence of 42 years. The 660 hours of survey effort generated during 2019-21 flight periods and 3908 people directly engaged through face-to-face events and activities – as well as millions more indirectly through television features such as British Broadcasting Corporation (BBC) Springwatch – brought a positive conservation story about our natural heritage to a broad demographic (O'Riordan, 2021).

Habitat across 16 managed sites in five Rockingham Forest networks is now in better condition and better managed for target species. We complemented Roots of Rockingham's achievements through this research project by proving that data sourced from museums, private butterfly collections, and historic texts are capable of reconstructing the decline of an extirpated butterfly species. Furthermore, we have shown how these data can be used to describe a pattern of loss in England, and how local extinction of *C. palaemon* colonies was buffered by site area and isolation to varying extents, emphasising the importance of habitat quality and defragmentation in the contemporary Rockingham Forest landscape. Additionally, we successfully trialled PMR on the reintroduced *C. palaemon* population at Fineshade Wood. Using photographs, we were able to study movements, dispersal, and lifespan of individual *C. palaemon* butterflies non-invasively, and estimate population size using capture-recapture histories. The 2019-21 daily population estimates can now be plotted against daily encounter rates and enhanced with 2022 data to generate a linear equation that will expedite the process of estimating population size in future years. Overall, we documented the history of *C. palaemon* in England chronologically from first English record at Clapham Park Wood in 1798 to final sighting in 1976, and eventual reintroduction in 2018. Our key findings illustrate the importance of historic data preservation and accessibility, and how conservation science can harness technological advancements to improve image-based population sampling of Lepidopteran species in the future.

# 8

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# 9

# Appendices

## Appendix 1: Additional Tables

**Table A1.1**: Butterfly species colloquial name, binomial name, and reintroduction location(s) (*=migrant or exotic species in reintroduction country).

| Colloquial name | Binomial name | Location(s) |
|---|---|---|
| Adonis blue | *Polyommatus bellargus* | UK and Ireland |
| Apollo | *Parnassius apollo* | Finland; Poland |
| baton blue | *Pseudophilotes baton schiffermuelleri* | Finland |
| bay checkerspot | *Euphydryas editha bayensis* | United States |
| black hairstreak | *Satyrium pruni* | UK and Ireland |
| black-veined white | *Aporia crataegi* | UK and Ireland |
| brimstone | *Gonepteryx rhamni* | UK and Ireland |
| brown argus | *Aricia agestis* | UK and Ireland |
| brown hairstreak | *Thecla betulae* | UK and Ireland |
| Camberwell beauty* | *Nymphalis antiopa* | UK and Ireland |
| chalkhill blue | *Polyommatus coridon* | UK and Ireland |
| chequered skipper | *Carterocephalus palaemon* | UK and Ireland |
| Chinese peacock* | *Papilio bianor* | UK and Ireland |
| Cleopatra* | *Gonepteryx cleopatra* | UK and Ireland |
| clouded Apollo | *Parnassius mnemosyne* | Finland |
| comma | *Polygonia c-album* | UK and Ireland |
| dark green fritillary | *Speyeria aglaja* | UK and Ireland |
| dingy skipper | *Erynnis tages* | UK and Ireland |
| Duke of Burgundy | *Hamearis lucina* | UK and Ireland |
| Esper’s marbled white | *Melanargia russiae* | Hungary |
| false ringlet | *Coenonympha oedippus* | Slovenia |
| gatekeeper | *Pyronia tithonus* | UK and Ireland |
| Glanville fritillary | *Melitaea cinxia* | UK and Ireland; Belgium; Finland; Netherlands |
| grayling | *Hipparchia semele* | UK and Ireland |
| green hairstreak | *Callophrys rubi* | UK and Ireland |
| grizzled skipper | *Pyrgus malvae* | UK and Ireland |
| heath fritillary | *Melitaea athalia* | UK and Ireland |
| high brown fritillary | *Fabriciana adippe* | UK and Ireland |
| Karner blue | *Lycaeides melissa samuelis* | United States |
| Lange’s metalmark | *Apodemia mormo langei* | United States |
| large blue | *Phengaris arion* | UK and Ireland; Netherlands |
| large copper | *Lycaena dispar* | UK and Ireland |
| large heath | *Coenonympha tullia* | UK and Ireland |
| large tortoiseshell | *Nymphalis polychloros* | UK and Ireland |
| Lulworth skipper | *Thymelicus acteon* | UK and Ireland |
| map* | *Araschnia levana* | UK and Ireland |
| marbled white | *Melanargia galathea* | UK and Ireland |
| marsh fritillary | *Euphydryas aurinia* | UK and Ireland; Germany |
| Miami blue | *Cyclargus thomasi bethunebakeri* | United States |
| mottled duskywing | *Erynnis martialis* | Canada |
| northern brown argus | *Aricia artaxerxes* | UK and Ireland |
| Oregon silverspot | *Speryeria zerene hippolyta* | United States |
| pearl-bordered fritillary | *Boloria euphrosyne* | UK and Ireland |
| purple copper | *Paralucia spinifera* | Australia |
| purple emperor | *Apatura iris* | UK and Ireland |

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|---|---|---|
| Quino checkerspot | *Euphydryas editha quino* | United States |
| red-dotted Apollo | *Parnassius bremeri* | South Korea |
| regal fritillary | *Speyeria idalia* | United States |
| Richmond birdwing | *Ornithoptera richmondia* | Australia |
| ringlet | *Aphantopus hyperantus* | UK and Ireland |
| scarce large blue | *Phengaris teleius* | Netherlands |
| scarce swallowtail* | *Iphiclides podalirius* | UK and Ireland |
| Schaus' swallowtail | *Papilio aristodemus* | United States |
| Scotch argus | *Erebia aethiops* | UK and Ireland |
| silver-spotted skipper | *Hesperia comma* | UK and Ireland |
| silver-studded blue | *Plebejus argus* | UK and Ireland |
| silver-washed fritillary | *Argynnis paphia* | UK and Ireland |
| small blue | *Cupido minimus* | UK and Ireland |
| small pearl-bordered fritillary | *Boloria selene* | UK and Ireland |
| small skipper | *Thymelicus sylvestris* | UK and Ireland |
| speckled wood | *Pararge aegeria* | UK and Ireland |
| swallowtail | *Papilio machaon* | UK and Ireland |
| Taylor's checkerspot | *Euphydryas editha taylori* | United States; Canada |
| violet fritillary* | *Boloria dia* | UK and Ireland |
| white admiral | *Limenitis camilla* | UK and Ireland |
| wood white | *Leptidea sinapis* | UK and Ireland |
| yellowish sedge-skipper | *Hesperilla flavescens* | Australia |

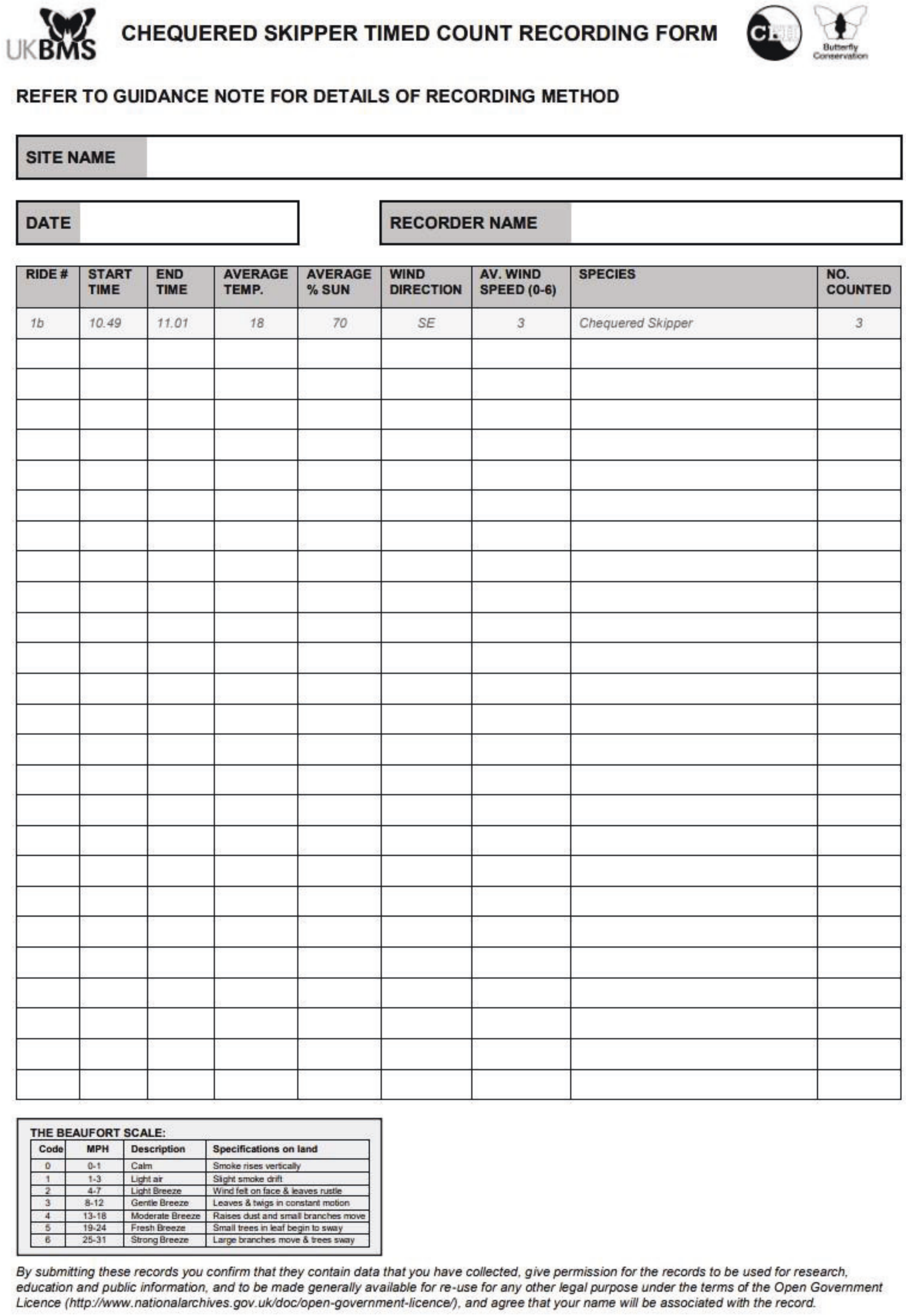
**Table A1.2**: Two-or-more years and records combined sites data used for 1-bp extinction trajectory plot and Spearman tests of association in SPSS.

| Site | Area (ha) | Total records | Last record | Duration (years) | Nearest site (m) |
|---|---|---|---|---|---|
| Gamlingay Wood | 49.8 | 5 | 1853 | 51 | 13,102.6 |
| Holme Fen | 269.4 | 3 | 1857 | 6 | 2,450.5 |
| Magog Down | 98.2 | 4 | 1878 | 29 | >20,000 |
| Wickenby Wood | 43.6 | 13 | 1897 | 1 | 3,286.7 |
| Lynwode Wood | 47.3 | 10 | 1925 | 29 | 138.2 |
| Harstholme Wood | 81.0 | 4 | 1929 | 29 | 3,020.0 |
| Stainton and Fulnetby Wood | 87.5 | 15 | 1942 | 23 | 742.1 |
| Bourne Wood | 307.1 | 3 | 1946 | 89 | 1,932.6 |
| Bearshank Wood | 47.9 | 2 | 1947 | 8 | 516.4 |
| College Wood | 70.7 | 3 | 1948 | 43 | 1,800.6 |
| Clapham Park Woods | 11.7 | 10 | 1949 | 151 | >20,000 |
| Coppice Leys and Culligalane Spinney | 17.7 | 11 | 1949 | 4 | 209.7 |
| Cadge and Hostage Wood | 86.3 | 2 | 1950 | 10 | 268.6 |
| Gibbs Wood | 13.4 | 2 | 1950 | 6 | 3,072.6 |
| Southwick Woods | 395.2 | 18 | 1950 | 50 | 274.1 |
| Jones' Covert | 29.2 | 2 | 1951 | 1 | 4,863.6 |
| Wardley Wood | 74.6 | 18 | 1951 | 92 | 4,528.1 |
| Mucklands Wood | 30.7 | 2 | 1954 | 4 | 2,637.0 |
| Grafton Park Wood | 140.8 | 4 | 1955 | 8 | 342.9 |
| Oakley Purlieus and South Wood | 150.0 | 26 | 1955 | 42 | 1,840.7 |
| Barnwell Wold | 55.3 | 83 | 1956 | 103 | 3,641.6 |
| Simon's and Oxey Wood + Helpston Heath | 55.5 | 9 | 1956 | 31 | 458.6 |
| Barnack Hills and Holes | 23.3 | 13 | 1957 | 52 | 1,304.5 |
| Morkery Wood | 170.2 | 7 | 1957 | 12 | 406.6 |
| Salome Wood | 24.0 | 3 | 1959 | 11 | 4,777.7 |
| Bushy Covert and Cranford Wood | 21.1 | 4 | 1960 | 13 | 763.4 |
| Stapleford Woods | 441.3 | 14 | 1960 | 103 | 10,749.4 |
| Laundimer Wood and Harry's Park Wood | 318.8 | 56 | 1961 | 59 | 390.7 |
| Holywell Wood | 179.7 | 4 | 1961 | 18 | 90.7 |
| Wakerley Woods | 320.6 | 414 | 1961 | 57 | 629.4 |
| Legsby Wood and Willingham Woods | 634.5 | 80 | 1962 | 106 | 130.0 |
| Fermyn Main Wood and Lady Wood | 144.5 | 388 | 1964 | 73 | 390.7 |
| Geddington Chase | 284.5 | 6 | 1964 | 62 | 525.0 |
| Sywell Wood | 98.3 | 5 | 1964 | 111 | 3,086.5 |

| | | | | | |
|---|---|---|---|---|---|
| Weekley Hall Wood | 171.6 | 7 | 1964 | 107 | 2023.6 |
| Wigsley Wood | 55.6 | 3 | 1964 | 30 | 4,470.4 |
| Southey Wood | 72.4 | 6 | 1965 | 14 | 285.5 |
| Woodwalton Fen | 209.1 | 35 | 1969 | 23 | 2,450.5 |
| Osgodby Wood | 384.6 | 2 | 1969 | 4 | 265.7 |
| Ashton Wold | 228.8 | 58 | 1970 | 117 | 3,641.6 |
| Newell Wood and Robert's Field | 107.4 | 7 | 1970 | 19 | 83.2 |
| Skellingthorpe Big Wood | 203.4 | 370 | 1970 | 127 | 3,020.0 |
| Bedford Purlieus | 214.3 | 162 | 1971 | 80 | 484.5 |
| Burley Wood | 206.1 | 2 | 1971 | 2 | 6,029.9 |
| Collyweston Great Wood and Eastern Hornstocks | 217.5 | 8 | 1971 | 43 | 203.8 |
| Monks Wood | 241.3 | 107 | 1971 | 42 | 3,295.6 |
| Ropsley Rise Wood | 57.7 | 8 | 1971 | 114 | 15,255.0 |
| Addah and Little Haw Wood | 72.4 | 4 | 1972 | 4 | 396.6 |
| Greetham Wood Near and Far | 108.1 | 6 | 1972 | 115 | 1,248.8 |
| Newball Wood | 118.9 | 58 | 1973 | 117 | 591.2 |
| Castor Hanglands | 181.9 | 677 | 1974 | 151 | 285.5 |
| Fineshade Wood | 574.1 | 286 | 1974 | 83 | 203.8 |
| Glapthorn Cow Pastures | 28.2 | 8 | 1975 | 88 | 771.1 |
| Ring Haw and Old Sulehay | 165.2 | 2 | 1976 | 46 | 624.1 |
| Luffenham Heath | 75.2 | 107 | 1976 | 44 | 143.5 |

# Appendix 2: Additional Figures

**A**



UKBMS **CHEQUERED SKIPPER TIMED COUNT RECORDING FORM** Butterfly Conservation

**REFER TO GUIDANCE NOTE FOR DETAILS OF RECORDING METHOD**

**SITE NAME**

**DATE**

**RECORDER NAME**

| RIDE # | START TIME | END TIME | AVERAGE TEMP. | AVERAGE % SUN | WIND DIRECTION | AV. WIND SPEED (0-6) | SPECIES | NO. COUNTED |
|---|---|---|---|---|---|---|---|---|
| *1b* | *10.49* | *11.01* | *18* | *70* | *SE* | *3* | *Chequered Skipper* | *3* |
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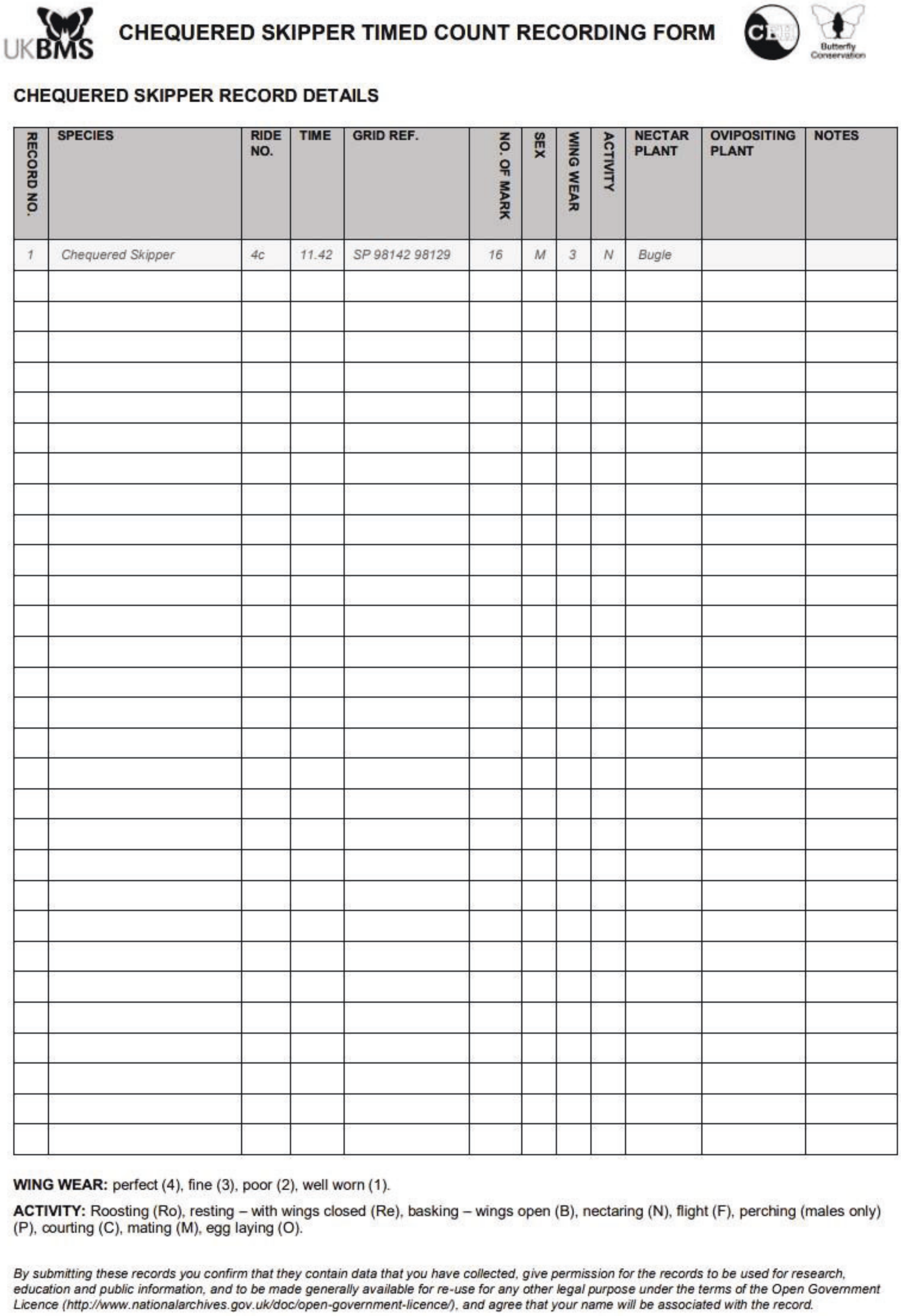
**THE BEAUFORT SCALE:**

| Code | MPH | Description | Specifications on land |
|---|---|---|---|
| 0 | 0-1 | Calm | Smoke rises vertically |
| 1 | 1-3 | Light air | Slight smoke drift |
| 2 | 4-7 | Light Breeze | Wind felt on face & leaves rustle |
| 3 | 8-12 | Gentle Breeze | Leaves & twigs in constant motion |
| 4 | 13-18 | Moderate Breeze | Raises dust and small branches move |
| 5 | 19-24 | Fresh Breeze | Small trees in leaf begin to sway |
| 6 | 25-31 | Strong Breeze | Large branches move & trees sway |

*By submitting these records you confirm that they contain data that you have collected, give permission for the records to be used for research, education and public information, and to be made generally available for re-use for any other legal purpose under the terms of the Open Government Licence (http://www.nationalarchives.gov.uk/doc/open-government-licence/), and agree that your name will be associated with the record.*

**B**



**CHEQUERED SKIPPER TIMED COUNT RECORDING FORM**

**CHEQUERED SKIPPER RECORD DETAILS**

| RECORD NO. | SPECIES | RIDE NO. | TIME | GRID REF. | NO. OF MARK | SEX | WING WEAR | ACTIVITY | NECTAR PLANT | OVIPOSITING PLANT | NOTES |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *1* | *Chequered Skipper* | *4c* | *11.42* | *SP 98142 98129* | *16* | *M* | *3* | *N* | *Bugle* | | |
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**WING WEAR:** perfect (4), fine (3), poor (2), well worn (1).

**ACTIVITY:** Roosting (Ro), resting – with wings closed (Re), basking – wings open (B), nectaring (N), flight (F), perching (males only) (P), courting (C), mating (M), egg laying (O).

*By submitting these records you confirm that they contain data that you have collected, give permission for the records to be used for research, education and public information, and to be made generally available for re-use for any other legal purpose under the terms of the Open Government Licence (http://www.nationalarchives.gov.uk/doc/open-government-licence/), and agree that your name will be associated with the record.*

**Figure A2.2**: United Kingdom Butterfly Monitoring Scheme (UKBMS) *C. palaemon* timed count recording forms (A and B) used by personnel at Fineshade Wood.

# Appendix 3: Museums and Natural History Societies

Bedford Museum: https://www.thehigginsbedford.org.uk/
Birmingham Museum and Art Gallery: https://www.birminghammuseums.org.uk/bmag
Bolton Museum and Archive Service: https://www.boltonlams.co.uk/
Brighton Museum and Art Gallery: https://brightonmuseums.org.uk/brighton/
Bristol City Museum and Art Gallery: https://www.bristolmuseums.org.uk/
Chelmsford and Essex Museum: https://www.chelmsford.gov.uk/museums/
Cliffe Castle Museum: https://www.bradfordmuseums.org/
Herbert Art Gallery and Museum: https://www.theherbert.org/
Dorset County Museum: https://www.dorsetmuseum.org/
Gallery Oldham: https://galleryoldham.org.uk/
Glasgow Museums: https://glasgowlife.org.uk/
Hampshire Cultural Trust and County Museums Service: https://www.hampshireculture.org.uk/
Hull City Museums and Art Galleries: https://www.hcandl.co.uk/museums-and-galleries/
Leeds Museums and Galleries: https://museumsandgalleries.leeds.gov.uk/
Leicester City Museums' Service: https://www.leicestermuseums.org/
Manchester Museum: https://www.museum.manchester.ac.uk/
Museum of Reading: https://www.readingmuseum.org.uk/
National Museums Liverpool: https://www.liverpoolmuseums.org.uk/
Natural History Museum, London: https://www.nhm.ac.uk/
Natural History Museum, Nottingham: https://wollatonhall.org.uk/hall-and-museum/natural-history-museum/
Northamptonshire Natural History Society: https://www.nnhs.info/
Oxford University Museum of Natural History: https://www.oumnh.ox.ac.uk/
Perth Museum and Art Gallery: https://www.culturepk.org.uk/museums-and-galleries/perth-museum-and-art-gallery/
Peterborough Museum and Art Gallery: https://cityculturepeterborough.org.uk/museum-art-gallery/
Plymouth City Museum and Art Gallery: https://www.theboxplymouth.com/
Portsmouth Museums and Records Service: https://portsmouthmuseums.co.uk/
Potteries Museum and Art Gallery, Stoke-on-Trent: https://www.stokemuseums.org.uk/pmag/
Royal Albert Memorial Museum, Exeter: https://rammuseum.org.uk/
Saffron Walden Museum: https://www.saffronwaldenmuseum.org/
Sheffield City Museum and Mappin Art Gallery: https://www.museums-sheffield.org.uk/
Tolston Memorial Museum: https://www.kirklees.gov.uk/beta/museums-and-galleries/tolson-museum.aspx

University Museum of Zoology, Cambridge: https://www.museum.zoo.cam.ac.uk/

Warwickshire Museum Service: https://heritage.warwickshire.gov.uk/museum

Wisbech and Fenland Museum: https://www.wisbechmuseum.org.uk/

Yale Peabody Museum: https://peabody.yale.edu/

## A3.1 Museum and Natural History Society Acknowledgements

Magdalene College, Cambridge data were provided by permission of the Master and Fellows of Magdalene College, Cambridge. Magdalene College, Cambridge, Wisbech and Fenland Museum, and University Museum of Zoology, Cambridge data were made available thanks to the Esmée Fairbairn collections fund run by the Museums Association. The Lancaster University *C. palaemon* specimens used in Chapter Three belong to a collection made by Edgar James Hare C.B.E. (1884-1969) that were donated by Mrs. Suzanne Hare in his memory.

We wish to thank the following for their help with data collection for Chapter Three: Clive Pratt, David Green, Adrian Russell, Susan Clarke, Michael Fuller, Douglas Goddard and Andy Wyldes (Butterfly Conservation Bedfordshire and Northamptonshire branch), Martin Izzard, John Robinson, Robyn Haggard (Glasgow Museums), Jeremy Mitchell, Neil Hagley, Ian Barnes (Natural History Museum, London), Richard Gill (Imperial College London), Holly Morgenroth (Royal Albert Memorial Museum), Angela Houghton (Museum of Reading), Mark Simmons (Perth Museum and Art Gallery), Steve Judd and Tony Hunter (National Museums Liverpool), Rosa Menendez Martinez (Lancaster University), Rhian Rowson (Bristol Museums, Galleries and Archives), Patricia Francis (Gallery Oldham), Abigail Padgett (Kirklees Museums and Galleries), James Lumbard (Saffron Walden Museum), Lukas Large (Birmingham Museums Trust), Glenn Roadley (Potteries Museum and Art Gallery), Matt Hayes (University Museum of Zoology, Cambridge), Christine Taylor (Portsmouth Museums and Records Service), Diana Arzuza Buelvas (Manchester Museum), Richard Gill (Imperial College London), Jon Philpott, Steve Meredith, Adrian Dutton, Paul Martin, Laura Trinogga (Doncaster Museum), Andy Barker (Butterfly Conservation Hampshire and Isle of Wight branch), Ross Turle (Hampshire Cultural Trust), Alison Clague (Leicestershire County Council Museum Collections), Heather Southorn (Leicester Museum and Art Gallery), Northamptonshire Natural History Society, and Lancashire and Cheshire Entomological Society.

# Appendix 4: Benefits of Woodland Management to Other Taxa

## A4.1 Introduction

The reintroduction of *C. palaemon* has improved knowledge of Lepidoptera, Odonata, Pentatomidae, and other flora and fauna present at Fineshade Wood thanks to an increase in survey effort since 2018. Fineshade Wood is considered to have been underrecorded for many years (D. James, personal communication). Adult *C. palaemon* timed counts, the creation of a UKBMS butterfly transect through managed and unmanaged woodland, moth surveying, moth trapping events, and various ecological surveys have resulted in the detection of dozens of new species at the site. Surveys elsewhere in Rockingham Forest led to the discovery of a wood white *Leptidea sinapis* colony at Geddington Chase, and isolated records from Weekley Hall Wood to its southwest suggest that further colonisation is possible. Ongoing management work at Geddington Chase is having a positive effect on its *L. sinapis* population. Woodland management and greater survey effort at Fineshade Wood – most of which instigated by Roots of Rockingham and latterly, Green Recovery Challenge Fund projects – are thought equally responsible for increased species richness and abundance.

## A4.2 Butterflies

Management work designed to improve habitat quality for *C. palaemon* and other hesperids has benefitted species with similar ecological requirements, as many butterflies prefer open, sunny, sheltered, herb-rich glades, and woodland rides (e.g. Warren, 1985; Tudor *et al.*, 2004; Fartmann *et al.*, 2013; Slamova *et al.*, 2021). Abundance of hesperids other than *C. palaemon* present at Fineshade Wood (large skipper *Ochlodes sylvanus*, dingy skipper *Erynnis tages*, grizzled skipper *Pyrgus malvae*, Essex skipper *Thymelicus lineola*, and small skipper *T. sylvestris*) increased in 2019 versus 2018 following the first winter of Back from the Brink habitat management works (Figure A4.1 – numbering conventions in appendices are the same as chapters, with an 'A' suffix to differentiate them). Abundance remained higher than pre-2019 through 2020 (the main pandemic-affected year) and 2021. The decline of hesperids in 2020 and 2021 versus 2019 may offer some indication of the true size of the *C. palaemon* population at the reintroduction site. Despite *C. palaemon* survey effort increasing in 2021 versus 2020, encounter rate decreased compared to the previous year. Total record abundance was similar in 2020 and 2021 (60 and 65 records, respectively), but lower than 2019 (173 records). In the absence of direct evidence, population trends of other hesperids – particularly *E. tages* and *P. malvae* – can act as indicators for *C. palaemon*. The flight periods of *E. tages* and *P. malvae* overlap with *C. palaemon*. Both species are conservation targets, and total survey effort has been similar to *C. palaemon*.

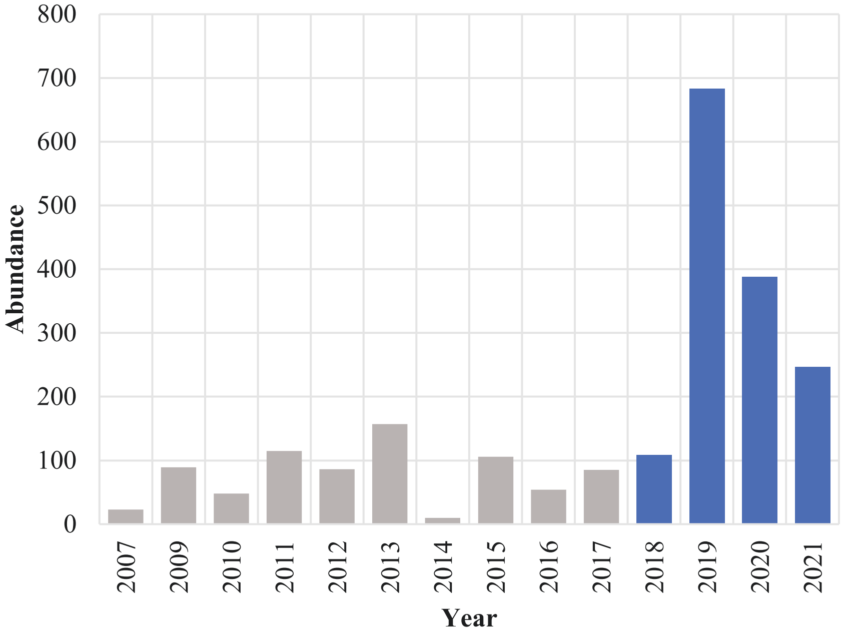


**Figure A4.1**: Annual adult Hesperiidae abundance at Fineshade Wood, 2007-21 (reintroduction project years in blue).

Abundance of *E. tages* peaked in 2019 (254 records), declining to 172 records in 2020 (-32.3%) and 118 records in 2021 (-31.4%) (Figure A4.2). *E. tages* fared better nationally (-11.0%, 2020-21) than at Fineshade Wood (UKBMS, 2021). *P. malvae* records fell to 59 in 2020 compared to 80 in 2019 (-26.3%), but recovered to 84 in 2021 (+42.4%), which outperformed the national index for the species (-17.0%). *E. tages* and *P. malvae* were recorded a total of 11 times from 2010-17 and 802 times from 2018-21 at Fineshade Wood. The late 2021 season in conjunction with *E. tages*' later flight period than *P. malvae* can explain the species' 31.4% decline in 2021. In 2020, *E. tages* was recorded 160 times in May and 12 times in June, but in 2021, a majority of records are from June (87), not May (31). Adult *C. palaemon* surveys ceased on June 13th in 2021, but *E. tages* was still recorded in good numbers up to this date. *E. tages* numbers typically peak in mid-June in England, and a late season would have further offset peak emergence from the *C. palaemon* survey window. Only two *E. tages* records are dated later than June 13th in 2021.

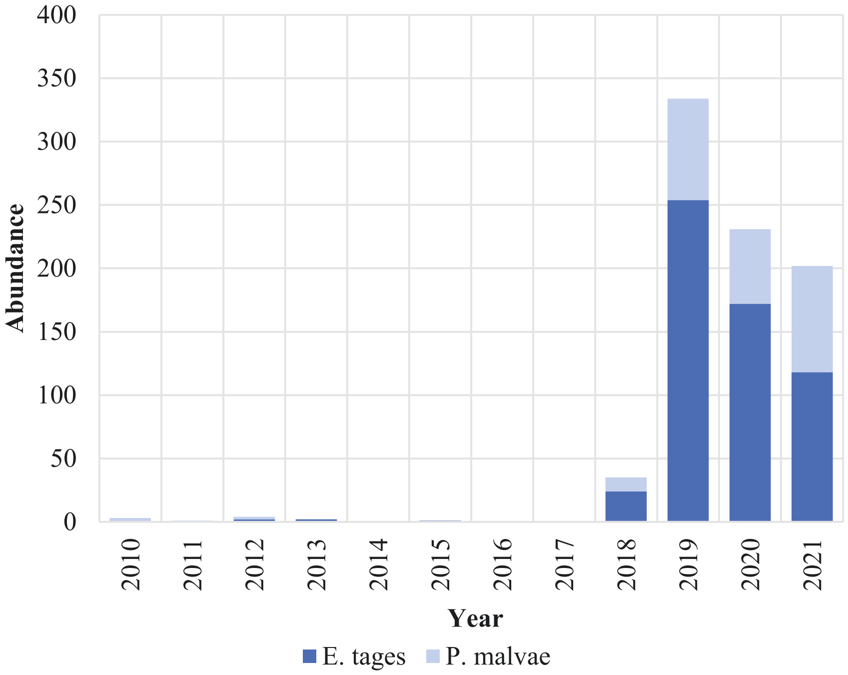


**Figure A4.2**: Annual adult dingy skipper *Erynnis tages* and grizzled skipper *Pyrgus malvae* abundance at Fineshade Wood, 2010-21.

The negative 2019-21 trend for hesperids bar *P. malvae* mirrors annual *C. palaemon* encounter rate decline, however abundance of all butterfly species at Fineshade Wood decreased during the same time period (Figure A4.3). Butterflies generally had a poor year in 2021 according to the UKBMS, indicating year-on-year decline was not caused by poor habitat suitability or unsuitable management practices specific to the reintroduction site. Decline in 2020 can be explained by survey effort reduction due to COVID-19.

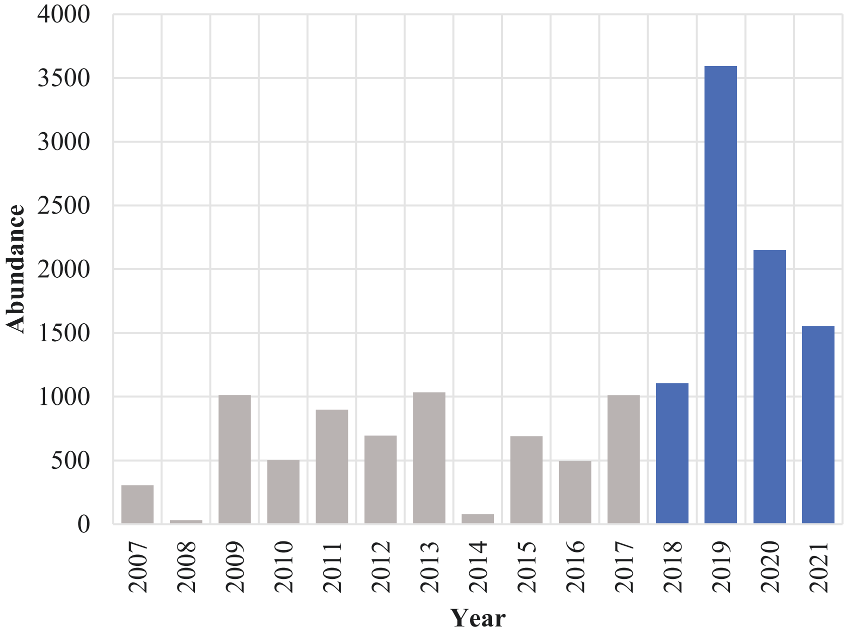


**Figure A4.3**: Annual adult butterfly abundance at Fineshade Wood, 2007-21 (reintroduction project years in blue).

The scale of direct impact of management at Fineshade Wood on other taxa is difficult to quantify due to historical underrecording and the uptick in survey effort and resolution of recording since 2018, however the creation of a managed-unmanaged habitat UKBMS transect walked by Susannah O'Riordan has enabled broad conclusions to be drawn. Total butterfly abundance in managed habitat in 2019 was 1,547, compared to 316 for unmanaged habitat. In 2020, abundance was 1,432 on managed and 293 on unmanaged. Total abundance declined to 816 on managed sections and 231 on unmanaged sections in 2021 (Figure A4.4). Survey effort was equal across both transects, indicating that habitat created by ride widening, scrub clearance, and mowing is preferred by a majority of butterfly species present at Fineshade Wood – more so than rides through part-coniferous high forest with closed canopies that shade out ground-level vegetation. Similarly, species richness is higher in managed habitat compared to unmanaged. In both 2019 and 2020, 16 species were recorded in unmanaged habitat, six (2019), eight (2020), and 11 (2021) species less than in managed habitat (Figure A4.5). *E. tages* and *P. malvae* were not detected on unmanaged sections from 2019-21.

**Figure A4.4**: Adult butterfly abundance on managed and unmanaged transect sections at Fineshade Wood, 2019-21.

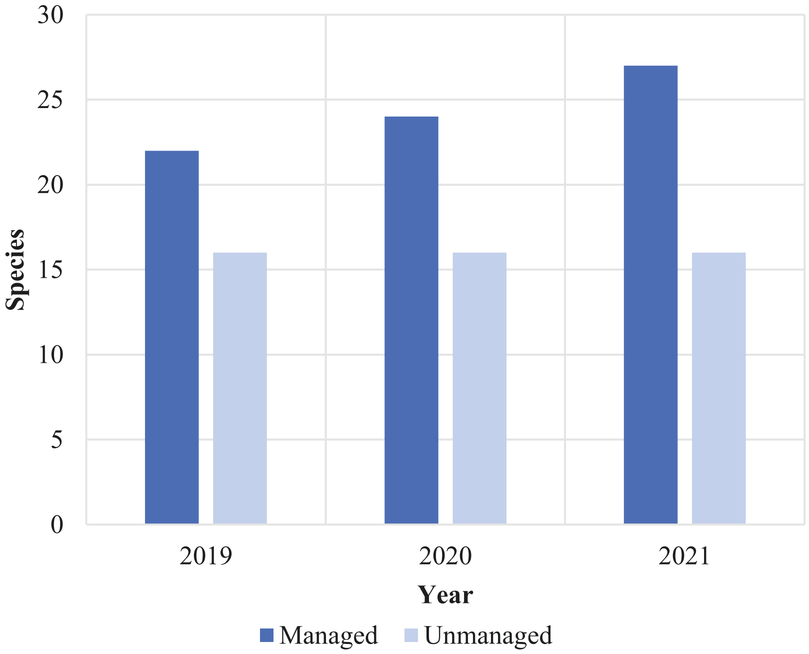


**Figure A4.5**: Butterfly species richness on managed and unmanaged transect sections at Fineshade Wood, 2019-21.

The dark-green fritillary *Speyeria aglaja* was first recorded at Fineshade Wood in 2018, and has been recorded each year since. A highly mobile species, it may have colonised the site from Ketton Quarry to the northwest, and found the damp, herb-rich woodland rides, and patches of bracken *Pteridium aquilinum* found at the reintroduction site to be suitable for occupation. The green hairstreak *Callophrys rubi* was observed in managed habitat in 2019 after last being recorded in 2012, and was again seen in both 2020 and 2021. Sunny scrub zones, ditch-edge bushes, bramble *Rubus fruticosus* agg., and common bird's-foot-trefoil *Lotus corniculatus* appear to be supporting a small colony. Since 2018, butterfly species richness at Fineshade Wood has increased, peaking at 33 in 2020 thanks to the presence of *C. rubi* and *S. aglaja*, the return of the black hairstreak *Satyrium pruni* (last recorded in 2009 before being recorded from 2018-20), regular recording of small copper *Lycaena phlaeas* and *P. malvae*, and reintroduction of *C. palaemon* (Figure A4.6). These species are all associated with woodland rides, clearings, and scrubby grassland, with *S. pruni* preferring dense, mature stands of *Prunus spinosa* found on sheltered, sunny woodland edges, but also gaps beneath the canopy of mature, open woodland (Bourn and Warren, 1998).

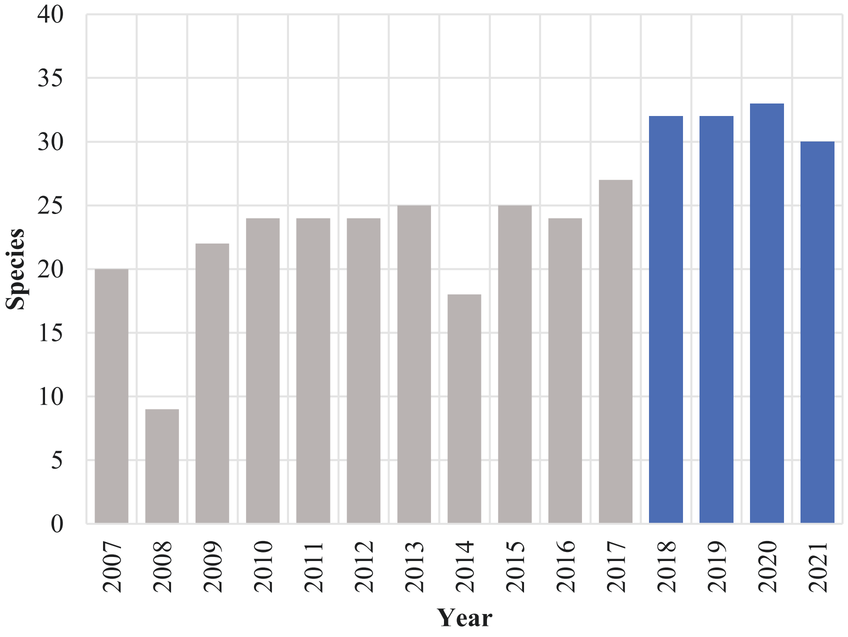


**Figure A4.6**: Annual butterfly species richness at Fineshade Wood, 2007-21 (reintroduction project years in blue).

## A4.3 Moths

The abundance of moth records at Fineshade Wood has increased since 2017. Total records exceeded 18,000 in 2018 and 10,500 in both 2020 and 2021 thanks to the efforts of Back from the Brink trappers and surveyors such as Ron Follows (Figure A4.7). From 2018 onward, annual species richness reached early 1990s levels when a Rothamsted Invertebrate Survey (RIS) light trap was in regular operation at the site (1993-2002). Over 450 species were recorded in 2018 and again in 2021, exceeding the previous peak of 447 species recorded in 1995 (Figure A4.8). Only 91 species were recorded between 2003-17. A strong relationship between presence and survey effort is again evident, given the lull in richness and abundance between RIS and Back from the Brink – Roots of Rockingham sampling.

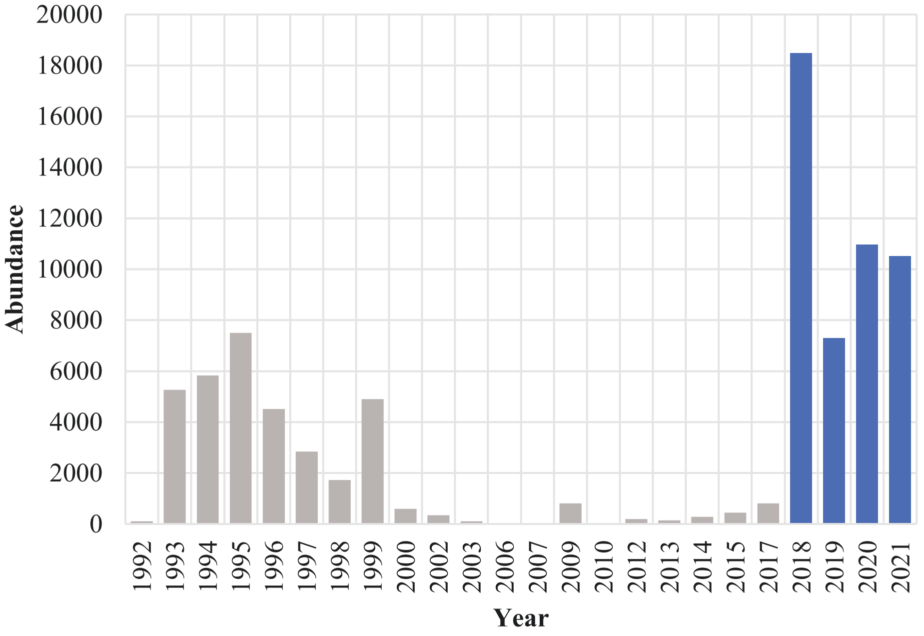


**Figure A4.7**: Annual moth abundance at Fineshade Wood for years data are available, 1992-2021 (reintroduction project years in blue).

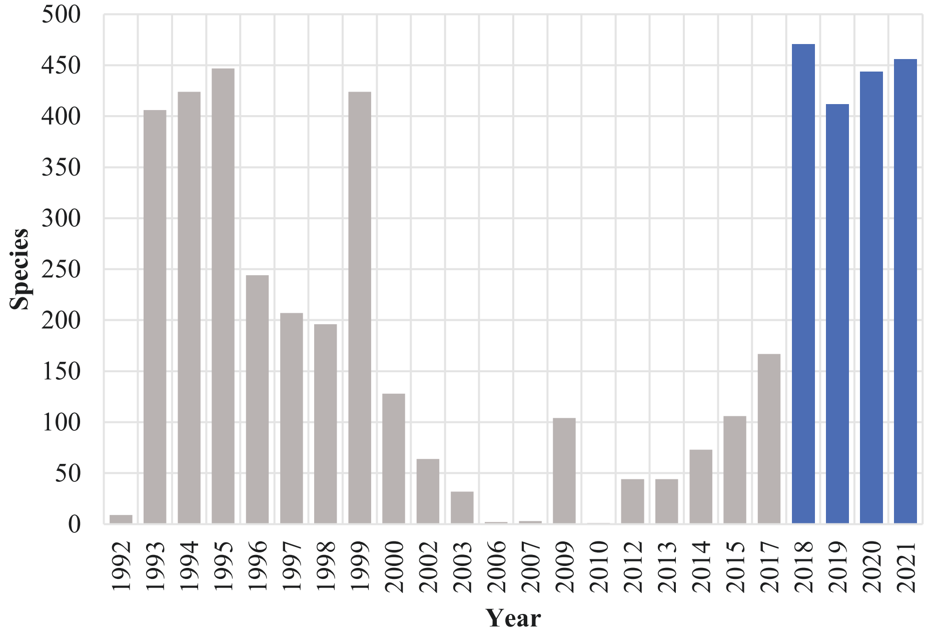


**Figure A4.8**: Annual moth species richness for years data are available, 1992-2021 (reintroduction project years in blue).

A total of 129 new species were recorded using moth traps placed around the reintroduction site between 2019-21 (64 in 2019, 38 in 2020, and 27 in 2021), including Nationally Scarce species *Pseudopostega crepusculella*, *Stathmopoda pedella*, *Assara terebrella*, *Pseudotelphusa scalella*, *Epinotia maculana*, and pine bud *Pseudococcyx turionella*, the rare *Anarsia innoxiella*, rare migrant tree-lichen beauty *Cryphia algae*, and migrants rusty-dot pearl *Udea ferrugalis*, Clifden nonpareil *Catocala fraxini*, and white-point *Mythimna albipuncta*. In 2017, the very local concolorous moth *Photedes extrema* was recorded at Fineshade Wood for the first time since 2003. A total of 251 *P. extrema* were trapped at the site the following year. *P. extrema* larvae feed internally on the stems of *Calamagrostis* spp., and the adult moth is principally found in wet woodland and marsh habitats (Pratt and Yates, 2000; Bentley, 2008). Habitat suitability is considered good for the species given the dominance of its *C. epigejos* hostplant in scrub zones. The influx of *C. fraxini* to Fineshade Wood has coincided with an increase in abundance and first records of other moth species more commonly associated with the south-east of England. This could be a result of climate change as much as ride management (R. Follows, personal communication).

## A4.4 Birds

A British Trust for Ornithology (BTO) transect has been in operation at Fineshade Wood since 2006. The 1km-square survey area is broken up into 10 sections: four adjacent to the managed reintroduction site (2-5) and six in unmanaged woodland and woodland edge habitat bordering farmland (1, 6-10). Although BTO transect effort is not equally distributed between managed and unmanaged habitat like the butterfly transect, the long-term data on abundance and species richness available still offers broad insight into the benefits of management to bird species. Since creation of the transect in 2006, 59 species of bird have been recorded in the 1km square during April-May and June-July surveys, with a record number of 43 species recorded in one year in 2015 (Figure A4.9). Management works have not resulted in a detectable increase or decrease in species richness since 2018. A total of 39 species were recorded annually on the transect between 2016-18, which increased to 41 in 2019 before falling slightly to 38 in 2020. Abundance on management-adjacent sections 2-5 is stable after 2017 with around 200 records per annum, more so than total abundance on unmanaged sections further south and west in coniferous woodland, which declined to 252 records in 2021 from totals of 314 and 318 records in 2019 and 2020, respectively (Figure A4.10). Total annual abundance on management-adjacent sections is lower than pre-management years 2012-16, but higher than 2006-11. The same is true for unmanaged sections. Much like richness, using BTO transect data, management has not had a clear positive or negative impact on abundance of bird species.

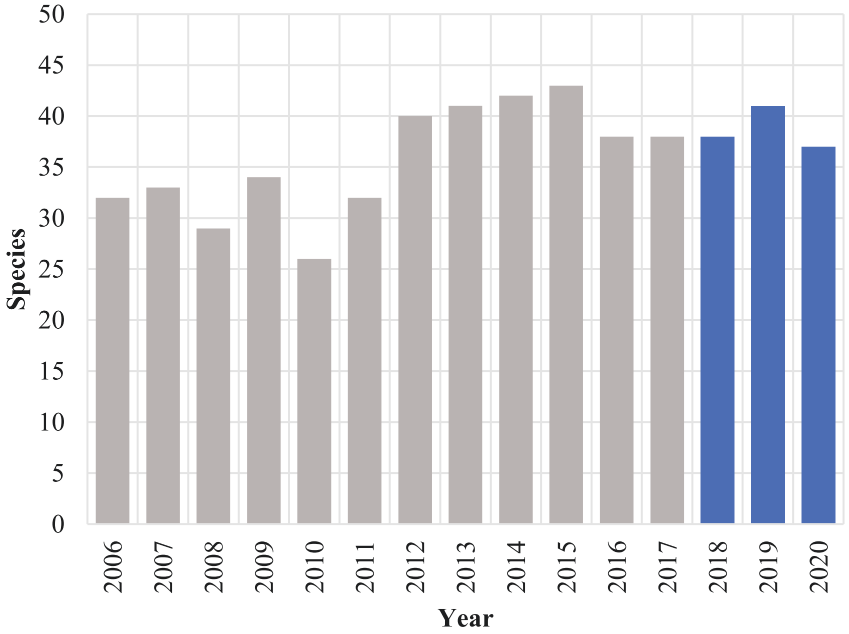


**Figure A4.9**: Annual bird species richness at Fineshade Wood, 2006-21 (reintroduction project years in blue).

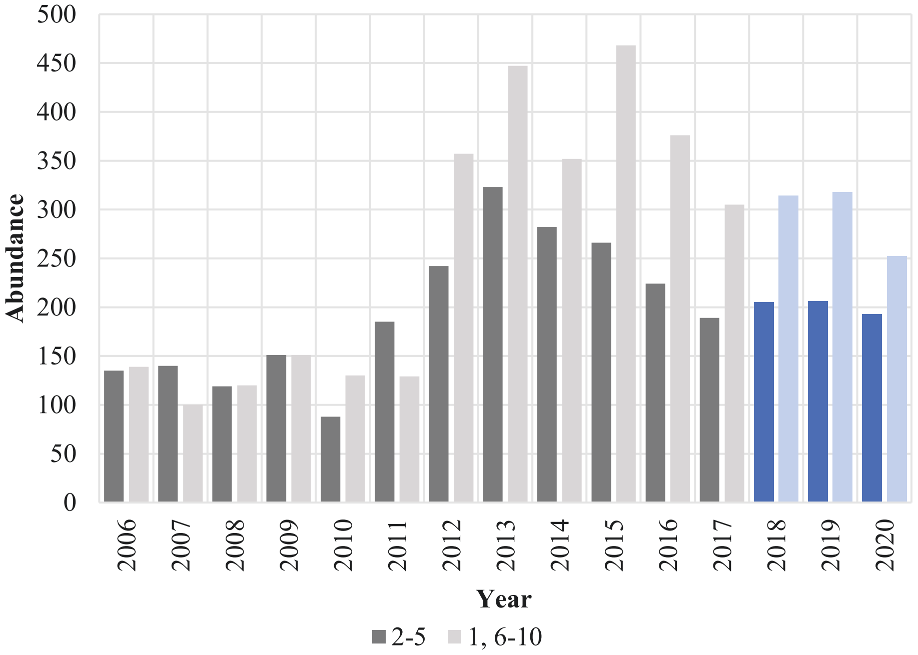


**Figure A4.10**: Annual bird abundance on managed (2-5) and unmanaged (1, 6-10) transect sections at Fineshade Wood, 2006-21 (reintroduction project years in dark and light blue).

The nightingale *Luscinia megarhynchos* (a Red List species – Standbury *et al.*, 2021) was heard at Fineshade Wood in 2013 and 2014. The bird was recorded again in 2017 after a break of three years, before regular detection in 2019, 2020, and 2021. *L. megarhynchos* favours low scrub, coppiced woodland, and young conifer plantations, and is chiefly a woodland edge species (Holden and Cleeves, 2002). Ride widening and scrub zone vegetation structure at Fineshade Wood may be providing more favourable conditions for the species. Experimental coppicing at woodland edges may benefit both *C. palaemon* and *L. megarhynchos*. Another Red List species, the grasshopper warbler *Locustella naevia*, was recorded from 2007-14, but not detected again until 2018. The bird's song was heard again in both 2019 and 2020, and it is now believed to have moved to occupy widened woodland rides (Galpin, 2022). *L. naevia* requires rich sources of invertebrate food such as beetles and lacewings near nesting sites (Holden and Cleeves, 2002). Increased food sources thanks to woodland management boosting invertebrate populations could explain why *L. naevia* is now being detected in adjacent woodland compartments. Back from the Brink – Roots of Rockingham surveys for willow tit *Poecile montanus* in 2018 (last recorded in 2011) failed to detect any in the wood, however this is reflective of a wider decline of *P. montanus* in England and not specific to the reintroduction site (Siriwardena, 2004; Lewis *et al*., 2007). A total of 102 bird species have been recorded at Fineshade Wood as of March 2021.

## A4.5 Other Flora and Fauna

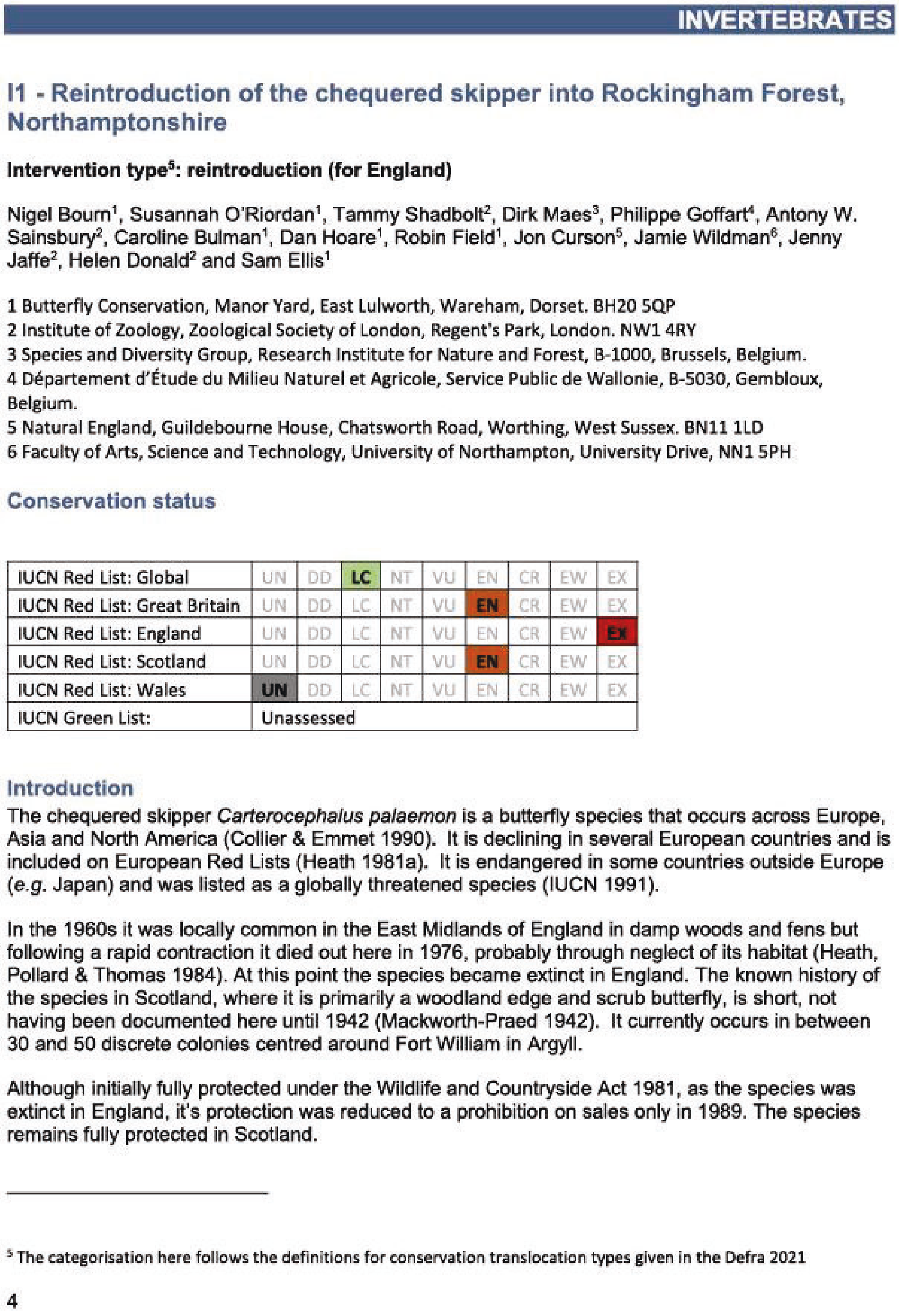
Purple small-reed *C. canescens* (a hostplant of *P. extrema*), ragged robin *Lychnis flos-cuculi* (*C. palaemon* nectar source), and heath false brome *Brachypodium pinnatum* (*C. palaemon* hostplant) (Ravenscroft, 1992; Joy and Bourn, 2000; Moore, 2004) have been located during vascular plant surveys (Handley, 2019). Rare in Northamptonshire species greater butterfly orchid *Platanthera chlorantha* (classified as Near Threatened on the Vascular Plant Red Data List for Great Britain – Cheffings *et al*., 2005), columbine *Aquilegia vulgaris*, and spreading meadow-grass *Poa humilis* are also present at the site in different woodland compartments (Handley, 2014; 2019). New invertebrate species were detected on managed rides at Fineshade Wood during adult *C. palaemon* timed counts between 2019-21, such as the hairy shield bug *Dolycoris baccarum* and white-legged damselfly *Platycnemis pennipes*.

A range of dragonfly species patrol rides and bask on ditch-edge scrub during *C. palaemon* timed counts, such as the broad-bodied chaser *Libellula depressa*, four-spotted chaser *L. quadrimaculata*, scarce chaser *L. fulva* (Near Threatened on the British Odonata Red List – Daguet *et al.*, 2008), emperor dragonfly *Anax imperator*, hairy dragonfly *Brachytron pratense*, and black-tailed skimmer *Orthetrum cancellatum*. A speckled wood *Pararge aegeria* was observed being systematically dismantled by *O. cancellatum* in 2020 after it had been predated by the dragonfly (Figure A4.11). The remains of a predated common blue *Polyommatus icarus* were found on a patch of bare ground on another ride section the same year (Figure A4.12). *C. palaemon* is potential prey for *O. cancellatum* and other dragonflies, however male *C. palaemon* were observed successfully evading chasing dragonflies in flight on two separate occasions. The first located an improvised perch on *J. effusus* inflorescence in the middle of a turf zone to evade capture, whereas the second ascended at speed to a height of approximately 10-15m before diving to grass height. The seasonal threat dragonflies present to butterfly assemblages at the reintroduction site should be assessed if habitat restoration has led to an increase in dragonfly abundance (e.g. Alonso-Mejia, 1994; Tiitsaar, 2013).

**Figure A4.11**: A) The body of a speckled wood butterfly *Pararge aegeria* in the mandibles of a black-tailed skimmer dragonfly *Orthetrum cancellatum*, and B) the butterfly's wing and antenna on leaf litter below the dragonfly's perch.

**Figure A4.12**: The remains of a predated ♂ common blue butterfly *Polyommatus icarus* at the junction of the hardcore track and a woodland ride at Fineshade Wood in 2020.

# Appendix 5: Papers in Press



**INVERTEBRATES**

## I1 - Reintroduction of the chequered skipper into Rockingham Forest, Northamptonshire

**Intervention type[5]: reintroduction (for England)**

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### Conservation status

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| IUCN Red List: Global | UN | DD | **LC** | NT | VU | EN | CR | EW | EX |
| IUCN Red List: Great Britain | UN | DD | LC | NT | VU | **EN** | CR | EW | EX |
| IUCN Red List: England | UN | DD | LC | NT | VU | EN | CR | EW | **EX** |
| IUCN Red List: Scotland | UN | DD | LC | NT | VU | **EN** | CR | EW | EX |
| IUCN Red List: Wales | **UN** | DD | LC | NT | VU | EN | CR | EW | EX |
| IUCN Green List: | Unassessed | | | | | | | | |

### Introduction

The chequered skipper *Carterocephalus palaemon* is a butterfly species that occurs across Europe, Asia and North America (Collier & Emmet 1990). It is declining in several European countries and is included on European Red Lists (Heath 1981a). It is endangered in some countries outside Europe (*e.g.* Japan) and was listed as a globally threatened species (IUCN 1991).

In the 1960s it was locally common in the East Midlands of England in damp woods and fens but following a rapid contraction it died out here in 1976, probably through neglect of its habitat (Heath, Pollard & Thomas 1984). At this point the species became extinct in England. The known history of the species in Scotland, where it is primarily a woodland edge and scrub butterfly, is short, not having been documented here until 1942 (Mackworth-Praed 1942). It currently occurs in between 30 and 50 discrete colonies centred around Fort William in Argyll.

Although initially fully protected under the Wildlife and Countryside Act 1981, as the species was extinct in England, it's protection was reduced to a prohibition on sales only in 1989. The species remains fully protected in Scotland.

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[5] The categorisation here follows the definitions for conservation translocation types given in the Defra 2021

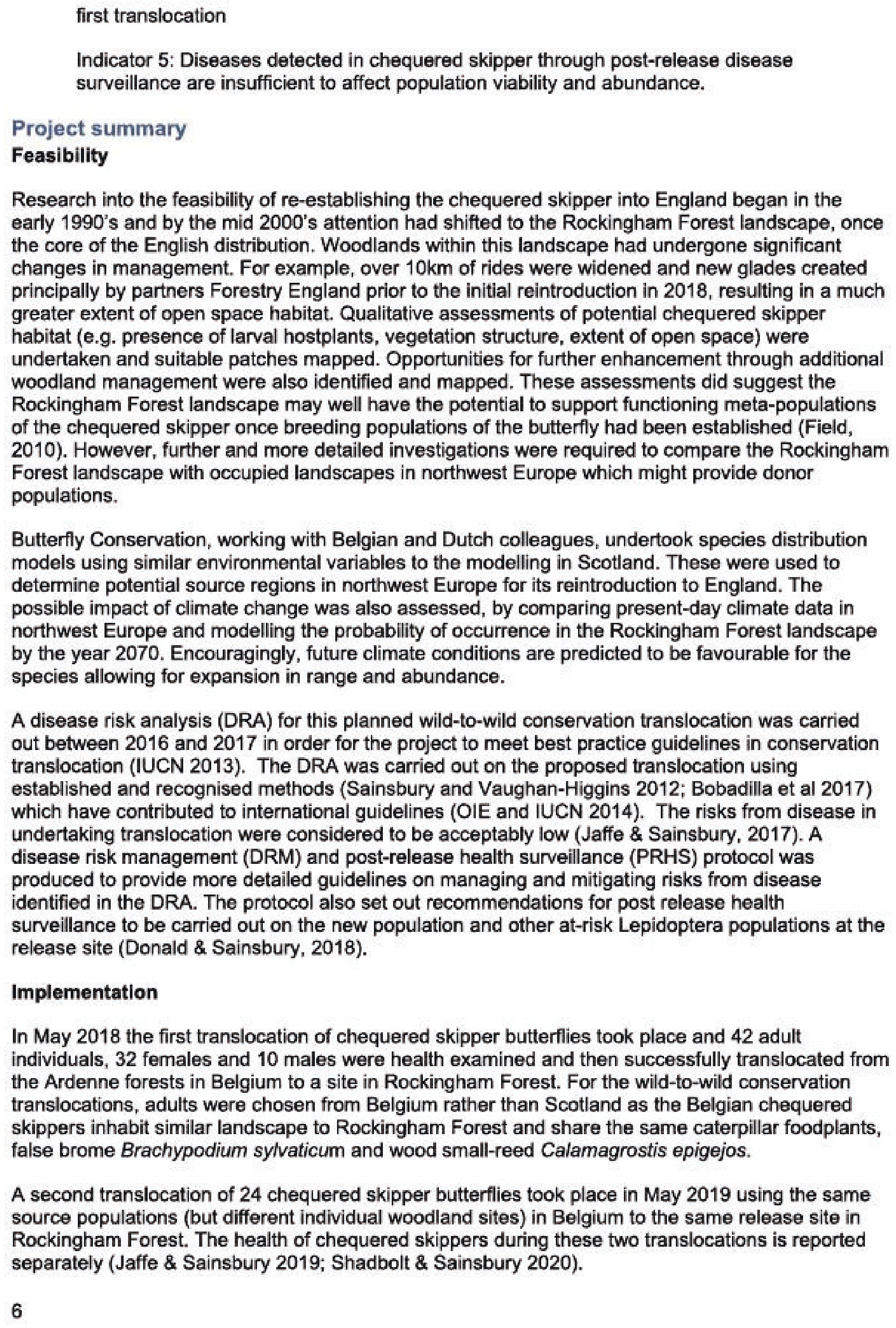
## Goals

- Goal 1: To establish a population of chequered skipper into a woodland site in England where it had previously been present;
- Goal 2: To establish a second population into a woodland site in the close vicinity;
- Goal 3: To establish a functioning meta-population consisting of several populations in one of 5 identified areas of Rockingham Forest in Northamptonshire that contain suitable sites for long term persistence;
- Goal 4: To establish a second functioning meta-population within several closely connected woodlands within Rockingham Forest; and
- Goal 5: To establish healthy populations of chequered skipper in England.

Figure 2 Chequered skipper (Image © Dave James, Butterfly Conservation)

## Success indicators

- Indicator 1: Establishment of a population in a site for 5 years
- Indicator 2: Establishment of a second population for 5 years
- Indicator 3: Sites being established independently of human intervention within the first area of establishment, indicating a functioning meta-population within 10 years of first translocation
- Indicator 4: Sites being established independently of human intervention within the second area of establishment, indicating a second functioning meta-population within 20 years of



first translocation

Indicator 5: Diseases detected in chequered skipper through post-release disease surveillance are insufficient to affect population viability and abundance.

## Project summary

### Feasibility

Research into the feasibility of re-establishing the chequered skipper into England began in the early 1990's and by the mid 2000's attention had shifted to the Rockingham Forest landscape, once the core of the English distribution. Woodlands within this landscape had undergone significant changes in management. For example, over 10km of rides were widened and new glades created principally by partners Forestry England prior to the initial reintroduction in 2018, resulting in a much greater extent of open space habitat. Qualitative assessments of potential chequered skipper habitat (e.g. presence of larval hostplants, vegetation structure, extent of open space) were undertaken and suitable patches mapped. Opportunities for further enhancement through additional woodland management were also identified and mapped. These assessments did suggest the Rockingham Forest landscape may well have the potential to support functioning meta-populations of the chequered skipper once breeding populations of the butterfly had been established (Field, 2010). However, further and more detailed investigations were required to compare the Rockingham Forest landscape with occupied landscapes in northwest Europe which might provide donor populations.

Butterfly Conservation, working with Belgian and Dutch colleagues, undertook species distribution models using similar environmental variables to the modelling in Scotland. These were used to determine potential source regions in northwest Europe for its reintroduction to England. The possible impact of climate change was also assessed, by comparing present-day climate data in northwest Europe and modelling the probability of occurrence in the Rockingham Forest landscape by the year 2070. Encouragingly, future climate conditions are predicted to be favourable for the species allowing for expansion in range and abundance.

A disease risk analysis (DRA) for this planned wild-to-wild conservation translocation was carried out between 2016 and 2017 in order for the project to meet best practice guidelines in conservation translocation (IUCN 2013). The DRA was carried out on the proposed translocation using established and recognised methods (Sainsbury and Vaughan-Higgins 2012; Bobadilla et al 2017) which have contributed to international guidelines (OIE and IUCN 2014). The risks from disease in undertaking translocation were considered to be acceptably low (Jaffe & Sainsbury, 2017). A disease risk management (DRM) and post-release health surveillance (PRHS) protocol was produced to provide more detailed guidelines on managing and mitigating risks from disease identified in the DRA. The protocol also set out recommendations for post release health surveillance to be carried out on the new population and other at-risk Lepidoptera populations at the release site (Donald & Sainsbury, 2018).

### Implementation

In May 2018 the first translocation of chequered skipper butterflies took place and 42 adult individuals, 32 females and 10 males were health examined and then successfully translocated from the Ardenne forests in Belgium to a site in Rockingham Forest. For the wild-to-wild conservation translocations, adults were chosen from Belgium rather than Scotland as the Belgian chequered skippers inhabit similar landscape to Rockingham Forest and share the same caterpillar foodplants, false brome *Brachypodium sylvaticum* and wood small-reed *Calamagrostis epigejos*.

A second translocation of 24 chequered skipper butterflies took place in May 2019 using the same source populations (but different individual woodland sites) in Belgium to the same release site in Rockingham Forest. The health of chequered skippers during these two translocations is reported separately (Jaffe & Sainsbury 2019; Shadbolt & Sainsbury 2020).

In 2020 a planned third translocation to a second site near the original release site was cancelled due to the global coronavirus (COVID-19) pandemic and re-scheduled for 2021.

Over 10km of rides were widened by partners, Forestry England prior to 2018 and a further 5km of ride widening took place between 2018-2020 on their estate. Since 2017, the National Lottery Heritage funded Back from the Brink project has enabled 6.5km of rides to be widened across several Rockingham Forest woodlands (owned/managed by Forestry Enterprise (FE), Bedfordshire, Cambridgeshire & Northamptonshire Wildlife Trust, Natural England), as well as 20km (20ha) of ride management and the creation of glades and temporary clearings further enhancing the area of open space habitat. These changes help to enable rotational mowing and thus maintain habitats in suitable condition. A further 10ha of ride are managed through Countryside Stewardship by the Boughton Estate.

**Post-release monitoring**

In 2018, Butterfly Conservation staff and volunteers monitored the chequered skipper adults at the release site from the moment the nets were removed on the morning of 24 May. The last adult to be observed post-release was seen on 6 June, so 14 to 15 days after collection in Belgium on 22 May. Though female egg laying behaviour (searching for suitable sites) was observed, no eggs could be detected amongst the dense vegetation.

Individual adults were not marked in this first year of translocations, meaning identification of individuals was only possible for one or two individuals who had distinctive wing wear. Sightings of butterflies indicated the dispersal of the released butterflies through the wood, with movement over 700 metres detected and regular movement over a 300-metre radius.

In 2019, population monitoring of adult butterflies during the flight period was again carried out by Butterfly Conservation staff and volunteers over a 40-day period from May to June. Figure 2 shows the distribution of butterfly sightings during the recording period. On 26th May 2019 24 butterflies translocated from Belgium were released at the site in Rockingham Forest. These were all marked with a red fine-tipped permanent marker pen to separate the two populations.

During the 2019 monitoring, there were a total of 124 sightings of un-marked chequered skipper butterflies, including 87 sightings of males, 25 of females and 12 of undetermined sex. A total of 34 sightings of marked chequered skippers from the 2019 release, including 23 of males, 10 of females and 1 of undetermined sex. In addition, there were 6 sightings of chequered skippers for which country of origin and sex could not be confirmed.

A maximum number of sightings on a single day was recorded on 30th May 2019 during which there were 12 un-marked butterfly observations, 13 marked butterfly observations and two observations of a butterfly of unknown origin. During the monitoring period there were no recorded health abnormalities, and no carcasses were submitted for post-mortem examination (Jaffe & Sainsbury 2019; Shadbolt & Sainsbury 2020). The butterfly had successfully spread throughout the ride network of the site, occupying approximately 3 kms of ride.

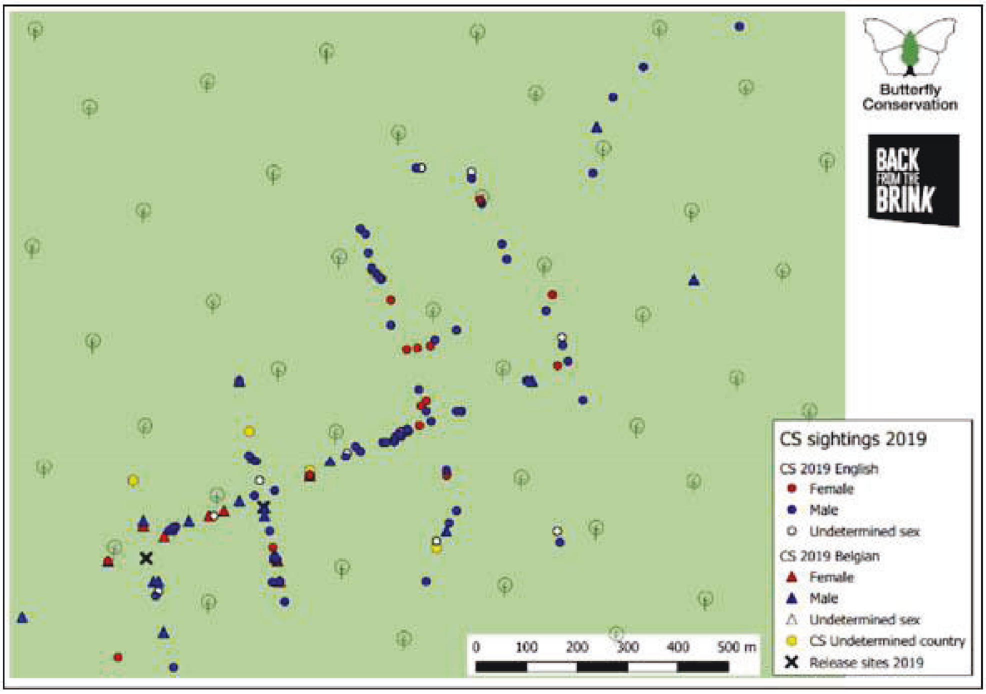


Figure 3 Distribution map showing sightings of adult chequered skipper butterflies during the monitoring period May to June 2019.

In 2020, restrictions due to COVID-19 prevented monitoring until the middle of May. The first sighting was on May 15th and the last sighting on May 31st. While overall numbers were lower, the peak count, 13 on the 19th, was higher than in 2018. The peak was also very soon after the first sighting. This and the short flight period observed during monitoring indicate that the butterflies had emerged much earlier than in 2019 and that emergence had been missed due to the limitations on monitoring. The lower number of male sightings also strongly suggests that the early part of the flight period was missed as males emerge before the females.

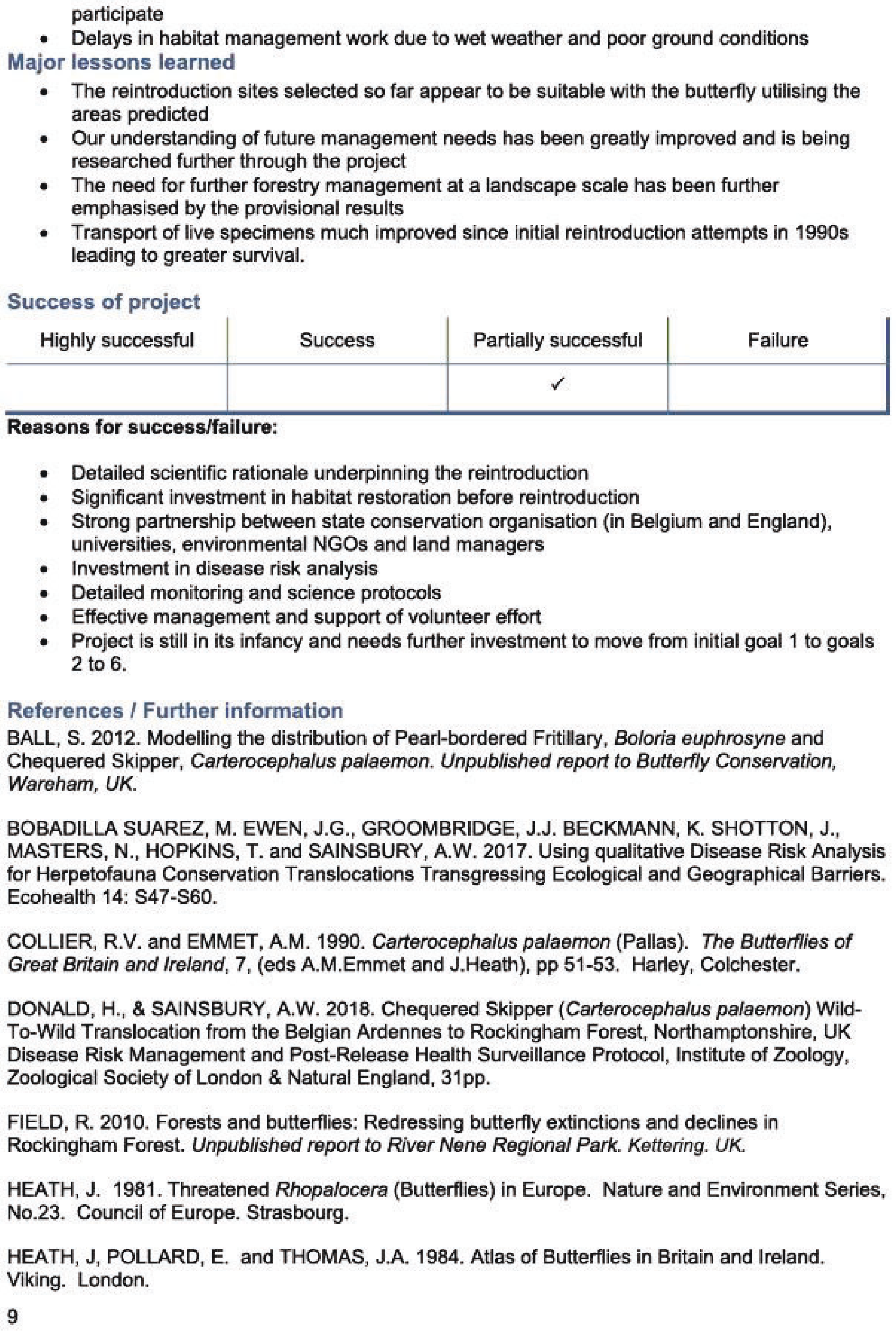
The distribution of adult butterflies throughout the introduction site, despite the lower numbers shows a similar area of occupancy in 2020. Although the monitoring was heavily impacted by the COVID-19 restrictions it does suggest, at least tentatively, that in order to secure goal 2 a further introduction will be required in the short term and, in the long term, surrounding forestry should be opened up with wider rides to facilitate the species dispersal.

The habitat management works undertaken for chequered skipper within Rockingham Forest have provided a wide range of biodiversity benefits through providing a more varied woodland structure and allowing light into the woodland benefitting plant and insects found in woodland edge habitats.

Monitoring of the chequered skipper population will continue long-term as part of the UK Butterfly Monitoring Scheme.

### Major difficulties faced

- Sufficient and long-term funding for the project to achieve all its goals
- Public interest in the project leading to interest in the location of the release site at a point when the population had yet to establish and would be potentially vulnerable to disturbance
- COVID-19 restrictions on field-work activity and on capacity of partners organisations to



participate

- Delays in habitat management work due to wet weather and poor ground conditions

### Major lessons learned

- The reintroduction sites selected so far appear to be suitable with the butterfly utilising the areas predicted
- Our understanding of future management needs has been greatly improved and is being researched further through the project
- The need for further forestry management at a landscape scale has been further emphasised by the provisional results
- Transport of live specimens much improved since initial reintroduction attempts in 1990s leading to greater survival.

### Success of project

| Highly successful | Success | Partially successful | Failure |
|---|---|---|---|
| | | ✓ | |

**Reasons for success/failure:**

- Detailed scientific rationale underpinning the reintroduction
- Significant investment in habitat restoration before reintroduction
- Strong partnership between state conservation organisation (in Belgium and England), universities, environmental NGOs and land managers
- Investment in disease risk analysis
- Detailed monitoring and science protocols
- Effective management and support of volunteer effort
- Project is still in its infancy and needs further investment to move from initial goal 1 to goals 2 to 6.

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