Biodiversity and Conservation (2024) 33:2011–2036
https://doi.org/10.1007/s10531-024-02837-6

ORIGINAL RESEARCH

Using photographic mark-recapture to estimate population size, movement, and lifespan of a reintroduced butterfly

Jamie P. Wildman[1,2] · **Jeff Ollerton**[1] · **Nigel A. D. Bourn**[2] · **Susannah O'Riordan**[2] · **Duncan McCollin**[1]

Received: 31 October 2023 / Revised: 18 March 2024 / Accepted: 27 March 2024 /

Abstract

The chequered skipper butterfly *Carterocephalus palaemon* was reintroduced to Fineshade Wood, England in 2018 as part of a Butterfly Conservation-led project following several years of planning. From 2019–2022, the population was sampled each May–June by the lead author, timed count volunteers, Butterfly Conservation staff, and casual observers. A novel photographic mark-recapture (PMR) technique was trialled as an alternative to mark-release-recapture (MRR). In conjunction with timed counts, PMR was used to photo-identify individual *C. palaemon* through each butterfly's upperside (ups) wing markings, estimate daily and gross population size, detect movements, and determine lifespan. As capture and recapture can be achieved non-invasively using PMR, habitat disturbance, the potential to influence butterfly behaviour, accelerate wing wear, affect mate selection and predation, and heighten mortality risk through handling are eliminated. We found PMR to be a viable alternative to MRR for a sensitive reintroduction of a low-density species with unique ups markings such as *C. palaemon*. Using capture histories generated through PMR, from a known founder population size of 42 butterflies in 2018, we estimated the population at Fineshade Wood had increased to 618 butterflies (+1371.43%) by 2022. Movements of up to 2.22 km over a time period of 17 days were also detected. Lastly, we discuss the implications of PMR for population sampling of other Lepidopterans, and the potential to improve cost-efficiency of the technique using machine-based learning tools.

Keywords *Carterocephalus palaemon* · Chequered skipper · Reintroduction · Photography · Photo-identification

---

Communicated by Louise Ashton.

✉ Jamie P. Wildman
jwildman@butterfly-conservation.org

[1] Faculty of Arts, Science and Technology, University of Northampton, Waterside Campus, Northampton NN1 5PH, UK

[2] Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP, UK

Introduction

Sampling techniques such as transect counts and mark-release-recapture (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 invertebrate taxon for which population trends can be best estimated in many parts of the world (e.g. de Heer et al. 2005; Thomas 2005; Hallmann et al. 2017; Seibold et al. 2019; van Swaay et al. 2019; Wepprich et al. 2019; Wagner et al. 2021; Fox et al. 2023; Ulrich et al. 2023). As butterfly species have annual lifecycles, they respond rapidly to environmental change, making changes in population health easy to detect 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 application of photo-identification to butterfly population studies has not yet been fully explored.

MRR is an established sampling technique that requires a butterfly to be captured in a net and its wings given a unique mark or number in ink, enabling later identification of the individual (see Ehrlich and Davidson 1960; Thomas 1983a; Murphy et al. 1986; Warren 1987; Williams 2002; Junker and Schmitt 2010; Pennekamp et al. 2014; Habel et al. 2018; Williams et al. 2018; Sielezniew et al. 2019; Hinneberg et al. 2023). 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 et al. 1987).

An experimental PMR technique was developed to estimate abundance of the chequered skipper butterfly *Carterocephalus palaemon* (Pallas 1771). *C. palaemon* is a univoltine species with a 29-31 mm wingspan that flies between May–June at lower altitudes, and July in mountainous areas of southern Europe above 1600 m (Higgins and Riley 1983; Tolman and Lewington 2008; Haahtela et al. 2011). It is colloquially known as the arctic skipper in North America (Bird et al. 1995). Male *C. palaemon* are territorial and take flight from perches offering good visibility of surrounding vegetation to chase off other males and invertebrates before circling back to the same perch or one nearby. Here they await mating opportunities with the more transient female (Ravenscroft 1992; Moore 2004; Thomas and Lewington 2016; Eeles 2019).

Females are more elusive 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 grasses such as wood small-reed *Calamagrostis epigejos* (Warren 1990), meadow foxtail *Alopecurus 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). Fletcher (1899) found that larvae “fed freely on all grasses offered to them, but seemed to prefer wide-leaved species” in former English populations, where *B. sylvaticum and B. pinnatum* were believed to be the main hostplants (Emmet and Heath 1989). *C. palaemon* is known to nectar on 18 species of flowering plant, but expresses a strong preference for blue, pink, purple, and white flowers such as bugle *Ajuga reptans*, bush vetch *Vicia sepium*, bluebell *Hyacinthoides non-scripta*, marsh thistle

Cirsium palustre, and bramble *Rubus fruticosus* agg. amongst others (Frohawk 1934; Farrell 1973; Collier 1978, 1986).

C. palaemon was declared extinct in England in 1976 after a precipitous decline beginning in the late 1940s-early 1950s (Wildman et al. 2022) caused by afforestation, coppicing abandonment, insufficient or 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, 1995; Moore 2004; Wildman 2023). 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 cool boxes, and released at Fineshade Wood within 48 h of capture. Further releases took place at the same site in 2019 and 2022.

PMR was preferred to MRR at Fineshade Wood to minimise trampling of suitable habitat (to set a precedent to the large number of volunteers undertaking timed counts on site), and due to low population density rendering traditional marking methods by a single person non-viable. Sampling intensity was therefore highly increased through collection of photographs taken by volunteers and visitors. PMR provided a unique opportunity to utilise photographs taken by a large number of volunteers, Butterfly Conservation staff, and casual recorders by adding them to those taken by the lead author during four May–June flight periods from 2019–22.

In this study, photographs are used to annually estimate the size of the reintroduced population, and minimum lifespans (duration between initial and last capture) and flight distances of individual butterflies. We aim to determine the efficacy of PMR as a non-invasive alternative to MRR population sampling and test our hypothesis that absolute population size can be estimated using a measure of encounter rate. We discuss our findings in relation to the ecology of *C. palaemon* at Fineshade Wood and consider population size, individual butterfly movements and lifespan derived from this technique in relation to other studies of *C. palaemon*. Lastly, we consider the potential for algorithm-based deep-learning PMR to assist with abundance, lifespan, and movement estimates for rare, endangered, or reintroduced (and hence likely to be vulnerable as they may not be fully established) butterfly species.

Methods

Population sampling

A detailed site map of 29 primary, secondary, and tertiary rides at Fineshade Wood was created, with each ride split into sections and assigned an alphanumeric code. Maps were given to recorders along with United Kingdom Butterfly Monitoring Scheme (UKBMS) *C. palaemon* timed count recording forms. Recorders were allocated walking routes in an attempt to ensure unbiased spatial and temporal coverage of the site, however primary and secondary rides still saw greater coverage than tertiary rides. Typically, between 10–26 sections were surveyed per recorder per day, depending on how long they remained on site, their pace, and work rate. This study was conducted over four consecutive flight periods to detect interannual fluctuations in population size, mobility, and lifespan rather than a single season, which would limit insight (e.g. Schtickzelle et al. 2002; Franzén et al. 2013; Nowicki 2017). The site was surveyed for 75 flight period days for a mean 10.2 h and maximum 29.2 h per day, excluding 10 days on which timed counts were cancelled. Rides were walked at a slow pace singularly or in pairs the centre of the rides to minimise habitat disturbance. When a native English or marked, translocated Belgian adult *C. palaemon* was detected, the time and location was recorded using an eight or 10-figure Ordnance Survey (OS) grid reference, it was sexed, its wing wear scored from four (perfect) to one (well-worn) and activity noted, as is typical in MMR studies (Thomas 1983a). Photographs were often taken during encounters, but not attempted in all cases due to the brevity of some sightings. Surveys were cancelled in the event of unsuitable weather. At the end of each flight period, a dataset of *C. palaemon* sightings was created using data transcribed from UKBMS forms and casual records submitted through email from trusted surveyors. Survey effort, *C. palaemon* encounter rate per ride section, and daily population indices were then calculated.

Photo-identification

Submitted images and those collated from verified sightings on iRecord (UKCEH 2022a) were converted to .jpg format when necessary and titles reformatted 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. Photos were visually assessed in chronological order, and individual specimens identified through differences in upper-forewing (upf) and upper-hindwing (unh) markings. Observer bias was not a factor during cataloguing as photo-identification was carried out by the lead author only.

Photos in which individual *C. palaemon* could be identified through unique wing patterns were then catalogued. 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 (but not uniquely to avoid undue disturbance to the butterfly) 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 original dataset. Image titles were not altered after cataloguing to ensure file provenance was preserved.

The variability of *C. palaemon* wing patterns, particularly gold markings in the upf discal cell and interspaces between subcoastal veins v10 and v4 in discal, postdiscal, and subapical wing areas enabled quick photo-identification of individuals. Three key upf marking groups were examined for variation (zones marked with 1, 2, and 3 in Fig. 1). Zone 1 (orange box) was interpreted as a solid gold triangle with a gap in its upper centre (if viewed from the same perspective as the image). This gap 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 zone 3 (blue box) – were often as distinctive.

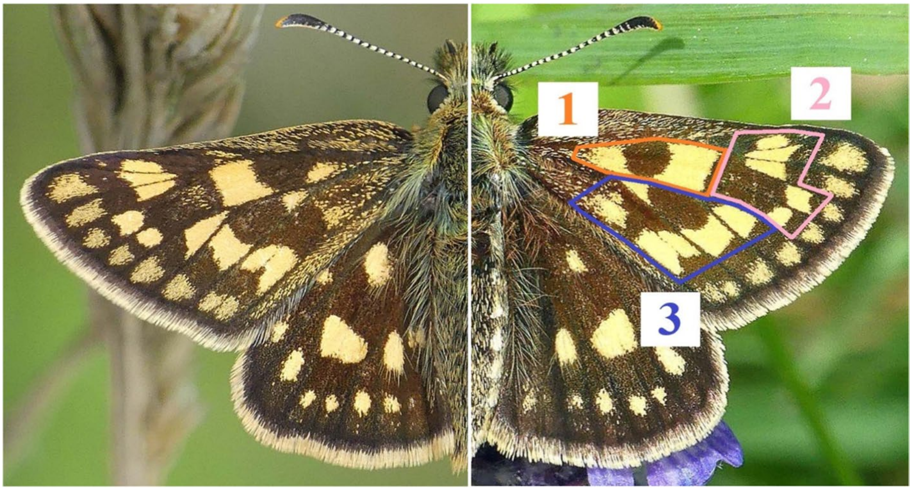


Fig. 1 Image of a *C. palaemon* specimen with distinctive upper-forewing (upf) pattern zones highlighted (right) and a different *C. palaemon* specimen (left) to illustrate variance in upf markings between butterflies (Image credit: David James and Andy Wyldes)

Markings in zones 1, 2, and 3 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. Using these zones, specimens up to 17 days old with a maximum wing wear of one could still be catalogued. Rather than making specimens harder to differentiate, wing wear and/or damage was another unique identifier than could be used to tell specimens apart, even in cases where markings in one or more of the three key zones were obfuscated. Providing upfs were visible in photographs of high enough quality, there were no examples where *C. palaemon* could not be catalogued, other than when only the right or left upf was visible. For example, a single specimen showing only its left upf in a photograph could not be determined to be a different butterfly from one showing only its right upf in absence of other distinguishing features such as wing damage. However, in a year where only one specimen was photographed showing either its right or left upf alone, its markings could not be confused with another specimen, and it was catalogued as normal.

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 differentiate markings by eye. Images were compared side-by-side, reoriented, and manipulated using Luminar 4 (Skylum Software 2020) to enhance quality when necessary. Uns-only, blurred, or low-resolution 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* seen on timed counts during the four flight periods, however it was impossible to say whether those sightings were of retrospectively known captured or recaptured specimens, or new butterflies that were never captured.

Movements

Geospatial and temporal data from catalogued images were entered on to worksheets according to sighting year. 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 (QGIS Development Team 2021) in .csv format. The FSC Biological Records Tool plugin (Field Studies Council 2022) was used to plot data as circular 10 m points (equivalent to an eight-figure OS grid reference) on a Google satellite map layer to standardise resolution. Straight line and ride-level measurements were taken between consecutive capture points, which is an established metric for describing the movements of recaptured butterflies (Fric and Konvička 2007; Junker and Schmitt 2010; Weyer and Schmitt 2013; Pennekamp et al. 2014; Ehl et al. 2019). Each movement was measured 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.

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-level 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, furthest observed distance from first capture point, and cumulative observed distance covered between all points for both straight line and ride-level.

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, and, for both straight line and ride-level: total distance covered, maximum distance from first capture, and maximum distance covered between any two captures. Using these data, mean distance between captures, mean distance covered per hour, and mean distance covered per day were calculated for each recaptured butterfly. Combined means for all male and females recaptured between 2019–22 were generated as well as separate means for males and females. A map of straight line movements between captures was created in QGIS.

Abundance

Once images were processed and catalogued, the specimen codes of individual native English *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:

00010011000100004;

Encounter histories for 2019–22 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 (2014). In 2018, the first reintroduction year, a founder population of 42 Belgian *C. palaemon* (32 females and 10 males) were released at Fineshade Wood. In 2019, a further 24 Belgian *C. palaemon* (12 males and 12 females) were released partway through the English flight period on Julian day 146 to supplement the population. Belgian *C. palaemon* capture-recapture data were excluded from all encounter rate calculations and population estimates to give a truer indication of the size of the native English population year-on-year.

The POPAN formulation – a parameterisation of the Jolly-Seber model (Schwarz and Arnason 1996) – 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 capture or 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.

Flight period was defined as the time period between first and last adult butterfly encounters (not captures and recaptures) for all years. 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 (*N*-hat*) population estimates were generated and saved to a .txt file.

Daily POPAN population size estimates were tested against site-wide *C. palaemon* encounter rates, a population index (Thomas 1983a), and total records per day using Spearman correlation in Statistical Project and Service Solutions (SPSS) (IBM Corp. 2021) to establish whether statistically significant relationships existed between the variables. Encounter rates were generated by transcribing handwritten UKBMS timed count data 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. All plots were created in Microsoft Excel (Microsoft Corporation 2021), bar the scatterplot, which was generated using ggplot (version 3.5.0) in RStudio (R version 4.3.3, R Core Team 2024).

Results

Population size

Population size was known in 2018 following the release of 42 adult *C. palaemon* (32 females and 10 males) at Fineshade Wood. The POPAN model estimated gross population size *N*-hat* at 314 native English butterflies in 2019 (SE: 4.32×10^5) (a 647.62% increase on 2018), 332 in 2020 (SE: 1.09×10^6), 721 in 2021 (SE: 3.38×10^6), and 618 in 2022 (SE: 8.27×10^5), marking a 1371.4% – or near 33-fold – increase in five years (Table 1). In 2019, the highest daily population estimate was 29.88 (SE: 11.19), 28.39 in 2020 (SE: 15.64), 13.64 in 2021 (SE: 5.74), and 21.36 in 2022 (SE: 7.62). From 2019–21, as expected, capture-recapture ratios were heavily biased to male *C. palaemon* (1.8:1 for captures and 3:1 for recaptures), whereas in 2022, a higher ratio of females than males were captured (1:0.7) and recaptures were split equally between sexes (1:1).

For native English *C. palaemon*, encounters per minute per day *Pmin*, total records per day *Rec*, and a daily population index *Idx* (calculated according to Thomas 1983a) 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 2019–22 study period. A total of 60 tests of association were carried out between variables and 34 found to be statistically significant. In 2022 and when data from all years (2019–2022) were combined, significant ρ-value correlations were found between *N-hat* (daily population size estimates generated through PMR histories) and *Rec* (total records per day), *Idx* (daily population index), and *Pmin* (*C. palaemon* encounters per minute per day). Paired sampled t-tests were performed with combined years *N-hat* correlated variables (*Pmin*: $t = 9.415$, $\rho = < 0.001$; *Rec*: $t = 3.687$, $\rho = < 0.001$; *Idx*: -8.423, $\rho = < 0.001$). Our hypothesis – that absolute population number calculated through PMR is correlated with a measure of encounter rate – was therefore correct.

The POPAN model indicated a sharp increase in abundance within 3–4 days of the start of each flight period (see Fig. 2). A classic bell-shaped curve was generated by the model in all years, which was expected given the butterfly's short flight period. This curve was less well-defined in both 2020 and 2021, but still comparable to conventional butterfly mark-release-recapture and capture-mark-recapture results (e.g. Ehrlich and Davidson 1960; Brussard 1971; Dempster 1971; Thomas 1983b; Warren 1995; Brereton 1997; Lewis et al. 1997; Roland et al. 2000; Hinneberg et al. 2022). Model estimates lagged behind actual increases in observations early in 2019 and 2020 but pre-empted increases towards population peaks in both 2021 and 2022. Elapsed time per *C. palaemon* encounter was lower in 2019 and 2020 (a mean of 67 min and 125 min, respectively) than 2021, where elapsed time per encounter rose to 292 min. In the following year, 2022, the mean halved to 146 min per sighting. 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.

Table 1 2019-22 Spearman correlation coefficients for *C. palaemon* population estimates against encounter rate, population index, and total records per day ($^{***}\rho = <0.001$, $^{**}\rho = <0.01$, $^{*}\rho = <0.05$)

Year	Gross population estimate (*N*-hat*)	Standard Error (SE)	Variable	Encounters per minute per day (*Pmin*)	Daily population estimate (*N-hat*)	Population index (*Idx*)	Total records per day (*Rec*)
2019	314.32	4.32×10^5	*Pmin*		0.251	0.534^{*}	0.640^{**}
			N-hat	0.251		0.280	0.383
			Idx	0.534^{*}	0.280		0.418
			Rec	0.640^{**}	0.383	0.418	
2020	332.27	1.09×10^6	*Pmin*		-0.035	0.090	0.638^{*}
			N-hat	-0.035		-0.242	-0.233
			Idx	0.090	-0.242		-0.119
			Rec	0.638^{*}	-0.233	-0.119	
2021	721.08	3.38×10^6	*Pmin*		0.386	-0.131	0.698^{***}
			N-hat	0.386		0.344	0.730^{***}
			Idx	-0.131	0.344		0.075
			Rec	0.698^{***}	0.730^{***}	0.075	
2022	618.35	8.27×10^5	*Pmin*		0.563^{**}	0.521^{*}	0.816^{**}
			N-hat	0.563^{**}		0.559^{**}	0.557^{**}
			Idx	0.521^{*}	0.559^{**}		0.604^{**}
			Rec	0.816^{**}	0.557^{**}	0.604^{**}	
All	N/A	N/A	*Pmin*		0.452^{***}	0.531^{***}	0.715^{***}
			N-hat	0.452^{***}		0.430^{***}	0.501^{***}
			Idx	0.531^{***}	0.430^{***}		0.503^{***}
			Rec	0.715^{***}	0.501^{***}	0.503^{***}	

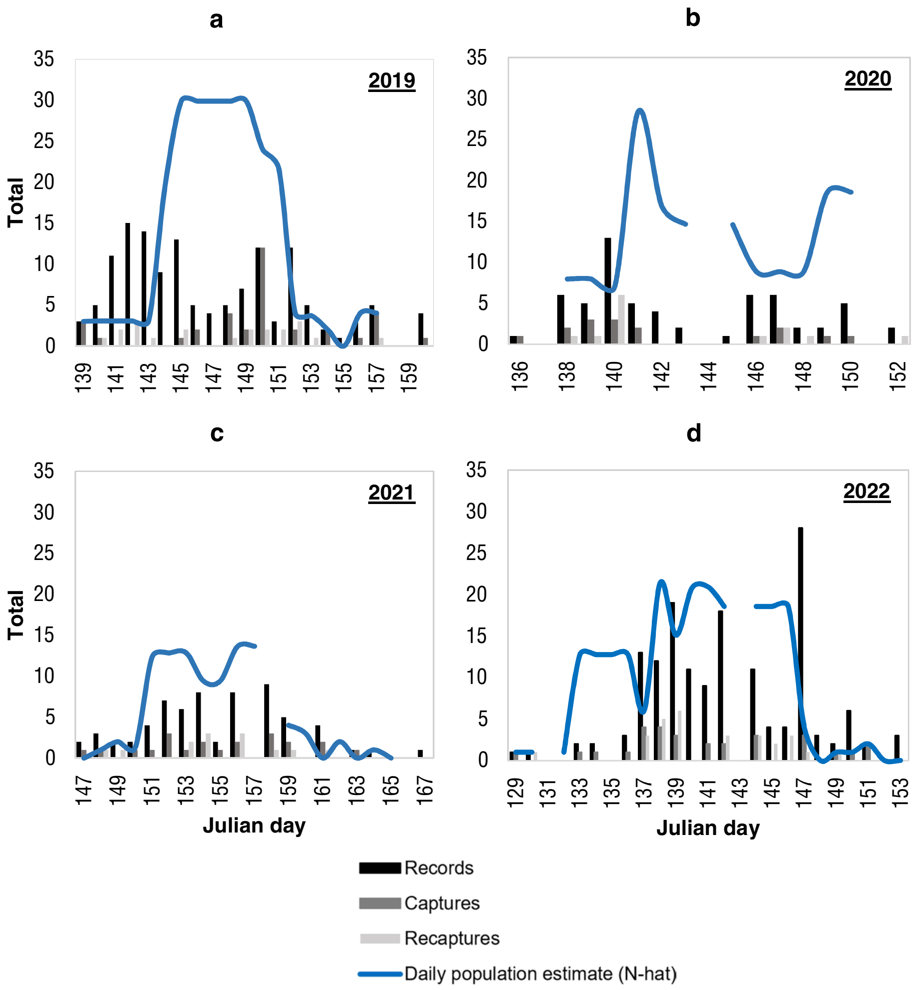


Fig. 2 Daily flight period records (native English *C. palaemon* only), photographic captures and recaptures, and POPAN model population size estimates (*N-hat*) per Julian day for **a** 2019, **b** 2020, **c** 2021, and **d** 2022 (note differences in horizontal axis scaling)

Daily records, capture, and recapture abundance remained low for all years, with records only exceeding 20 per day twice. Captures per day reached double figures on one occasion, and there were never more than six recaptures in a day. Larger totals were seen in 2019 and 2022 than 2020–21, with capture and/or recapture events occurring on 17 days in both years, compared to 11 in 2020 and 14 in 2021. A mean 2.1 captures and/or recaptures occurred per day for all years, and 0.9 per day for recaptures alone. These values were negatively affected by days with no survey effort, such as in 2021, where monitoring was suspended at the presumed end of the flight period, however a casual survey three days later resulted in a *C. palaemon* record that extended it. On occasion, survey effort was cancelled due to poor weather or when volunteers were unavailable.

Gross capture-recapture rates

Over the four flight periods (2019–22), 453 *C. palaemon* records were submitted. Of these 453 records, 101 individual native English and translocated Belgian *C. palaemon* were photo-identified (i.e. captured) (Table 2), meaning that 22.3% of all recorded *C. palaemon* were captured using PMR. Of these 101 individuals, 44 (39.6%) were recaptured (i.e. identified using a photograph taken during a previous encounter) and 75 movements detected (Fig. 3). In total, twenty-three *C. palaemon* were recaptured once, thirteen were recaptured twice, six were recaptured three times, and two were recaptured four times. Only two Belgian *C. palaemon* – a male and a female – were recaptured one time each

Table 2 Total native English and translocated Belgian *C. palaemon* records, photographic-mark-recapture (PMR) captures and recaptures at Fineshade Wood, 2019–22

Year	Total records	Total captured	% captured	Female-male capture ratio	Total recaptured	% recaptured	Female-male recapture ratio	Total recaptures
2019	173	35	20.2	1:1.7	11	31.4	1:2.7	21
2020	60	16	26.7	1:1.7	9	56.6	1:3.0	13
2021	65	21	32.3	1:2.0	10	47.6	1:3.3	13
2022	155	29	18.7	1:0.7	14	48.3	1:1.0	28
Overall	*453*	*101*	*22.3*	*1:1.4*	*44*	*45.9*	*1:1.8*	*75*

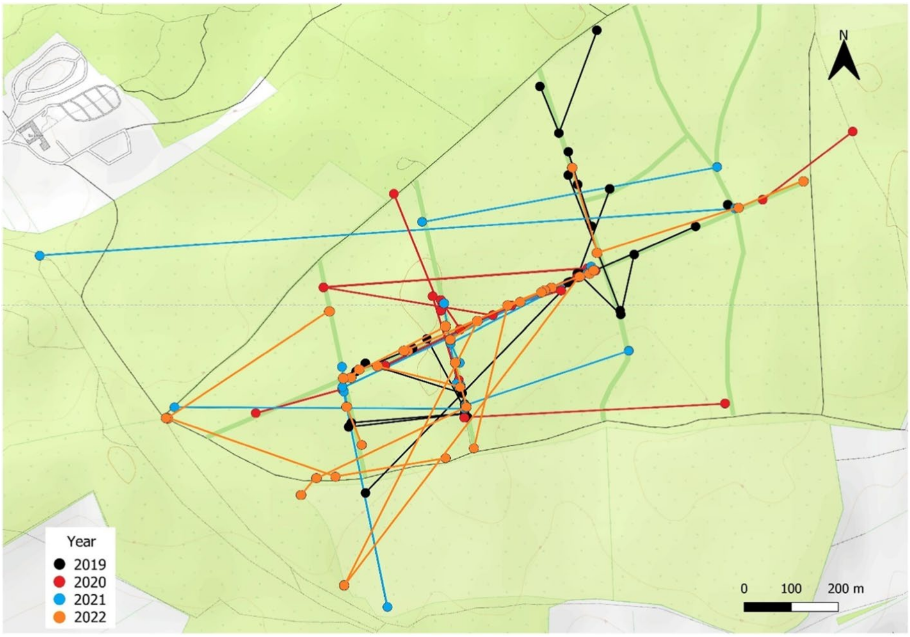


Fig. 3 Photographic mark-recaptured male and female English and Belgian *C. palaemon* movements at Fineshade Wood, 2019–22 ($n=75$). Each point represents an eight or ten-figure OS grid reference at which an individual was captured or recaptured. Straight lines connect points in order from initial capture to last recapture

Table 3 2019 native English *C. palaemon* and translocated Belgian *C. palaemon* records, photographic-mark-recapture (PMR) captures and recaptures. This table does not include eight *C. palaemon* sightings of unknown sex in 2019 or 2022 data, as only five Belgian *C. palaemon* were released at Fineshade Wood and none were recaptured that year

Origin	Total records	Total captured	% captured	Female-male capture ratio	Total recaptured	% recaptured	Female-male recapture ratio	Total recaptures
Belgium	35	10	28.6	1:2.1	2	20.0	1:1	2
England	130	25	19.2	1:1	9	36.0	1:3.5	19

in 2019 (Table 3). A higher ratio of males than females were captured (1.4:1) and recaptured (1.8:1) across the four flight periods. 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 captured specimens (-54.3% in 2020 and -40.0% in 2021). Records more than doubled in 2022 to 155 and total captures rose to 29 – only six less than in 2019 (a year in which 24 Belgian *C. palaemon* were released). Despite fewer butterflies being captured in 2022 compared to 2019, more were recaptured (14 versus 11) – an increase of 16.9%. Notably, in 2019, 2020, and 2021, female:male capture and recapture ratios were heavily biased to males, however in 2022, more females were captured than males, and recaptures were equally split between sexes. Total recaptured specimens remained relatively stable despite the large variance in total records submitted across the four flight periods. 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 (Fig. 4).

Twenty-one specimens were recaptured more than once: 13 were recaptured twice, six recaptured three times, and two recaptured four times. A 2019 female (1901F) and 2022 male (2201M) were recaptured four times over 290-h (12 day) and 406-h (17 day) periods respectively (Fig. 4). 2201M was only recaptured twice during a 14-day spell, during which he moved a minimum of 2,055 m from the centre of the release site to its southwestern edge and back again. Another male, 2106M, was only recaptured once, over 100 h after initial capture. Minimum lifespans of 14 of the 44 recaptured specimens (31.8%) exceeded 96 h or four days, whilst 18 were recaptured < 24 h apart (40.9%) – eight on the same day. Elapsed time between captures was rounded down to the nearest whole hour, therefore the minimum lifespan of three specimens was stated as zero.

Movements and lifespan of individual butterflies

The mean observed minimum lifespan of all recaptured *C. palaemon* across the three flight periods was 77.1 h (72.1 h for males and 76.8 h for females). Lifespan of the three specimens that exceeded 10 days were 265 h (11 days), 290 h (12 days), and > 406 h (16.9–17 days), respectively (Fig. 5). The exact lifespan of the 406-h specimen, 2206M, was unknown, as he was last recaptured during a three-hour window on the 17th day following initial capture, so the minimum duration was chosen. Mean lifespan for male and female *C. palaemon* decreased from 80.4 h in 2019 to 67.4 h in 2020 and 50.2 h in 2021, before almost doubling to 99.9 h in 2022. Based on straight line measurement, males flew

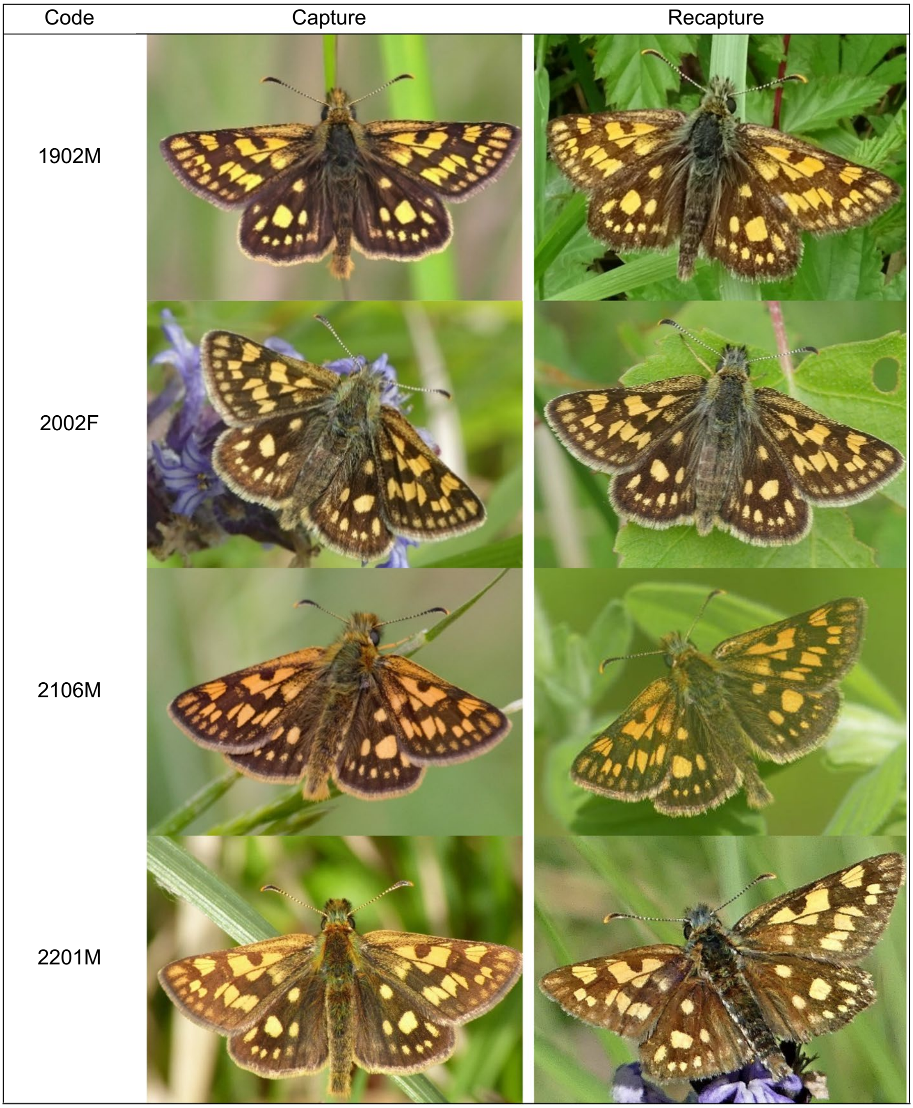
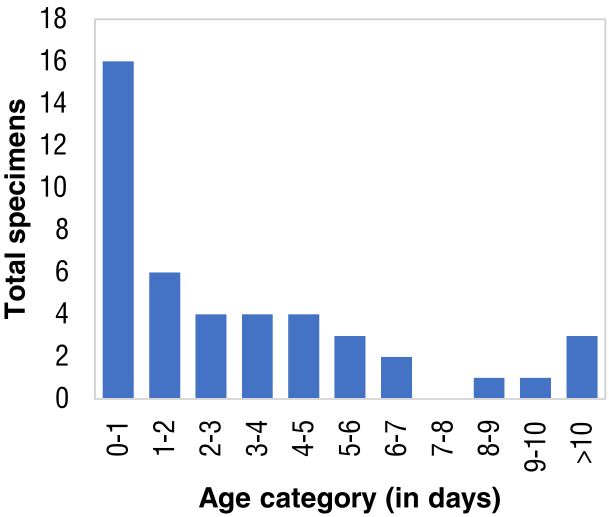


Fig. 4 An example *C. palaemon* capture-recapture from each of the four studied flight periods at Fineshade Wood (2019, 2020, 2021, and 2022) (Image credit: David James, David and Sally Irven, Andy Wyldes, Nick Freeman, Paul Fisher, Roger and Sarah Orbell)

a mean distance of 390 m in 2019, 288.3 m in 2020, 590.6 m in 2021, and 485 in 2022 (438.5 m for all years combined). Females flew a mean total distance of 200.3 m in 2019, 637.3 m in 2020, 183.7 m in 2021, and 298.3 m in 2022 (329.9 m for all years combined). A total of three specimens (2106M, 2103M, and 2201M) each flew > 1,000 m (Fig. 6).

Using ride-level measurement, six specimens travelled > 1,000 m. Males flew a mean distance of 495 m in 2019, 318.5 m in 2020, 768.6 m in 2021, and 631 m in 2022 (553.3 m for all years combined). Females flew a mean total distance of 231 m in 2019, 802.3 m

Fig. 5 Lifespan of recaptured *C. palaemon* butterflies at Fineshade Wood, 2019–22



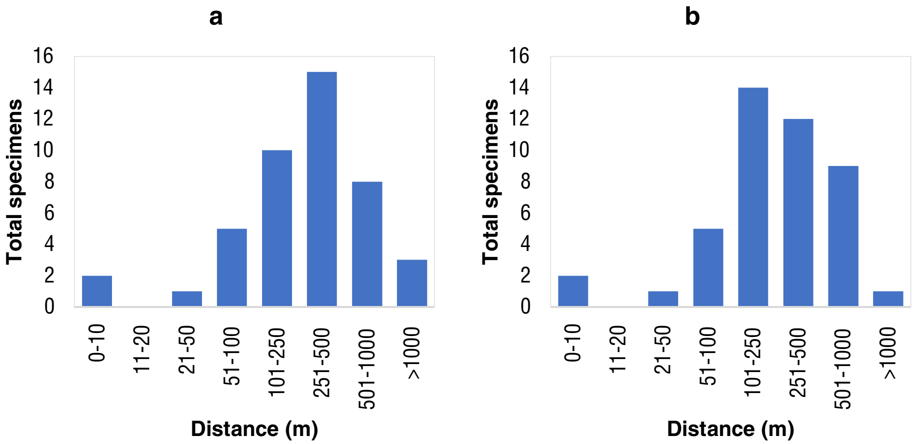


Fig. 6 Total distance covered by recaptured (**a**) and furthest distance from initial capture (**b**) *C. palaemon* using straight line measurement at Fineshade Wood, 2019–22

in 2020, 159 m in 2021, and 316.1 m in 2022 (377.1 m for all years combined). Means for both distance metrics were calculated from three recaptured females per year in 2019, 2020, and 2021, and seven in 2022. For males, means were calculated from eight recaptured specimens in 2019, six in 2020, and seven in both 2021 and 2022. When data from both sexes were combined, mean total distance covered was 487.7 m using ride-level measurement, and 398.5 m using straight line measurement (Table 4). The largest distance travelled was 1,630 m using straight line measurement and 2,222 m using ride-level measurement by 2201M. Large total distances were not achieved solely over multiple days: distances of 664 m, 1,010 m, and 1,341 m were covered by three specimens (2002F, 2003F,

Table 4 Mean movements using ride-level and straight line measurement for male and female *C. palaemon* at Fineshade Wood, 2019–22

Measurement	Distance covered (m)	Distance from first capture (m)	Distance between captures (m)	Distance per hour (m)	Distance per day (m)
Ride-level	487.7	403.3	305.0	47.9	191.9
Straight line	398.5	330.6	250.9	35.7	161.0

and 2109M) in a mean time of 24 h, as determined by ride-level measurement. One specimen, 2104M, was measured to have travelled 888 m in one hour using the same metric.

Discussion

Mobility, dispersal, and population size

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) due to low population density and the small size of the reintroduced *C. palaemon* population compared to other colonial species. Sampling in 2020 was reduced due to COVID-19 social distancing and travel restrictions on non-essential journeys. Although ride sections were still surveyed for up to a combined 16 h per day for over two weeks, density and frequency of coverage per day was compromised by an overall lack of site presence (for comparison, maximum survey effort in one day in 2022 was 29.2 h). Timed counts were delayed by COVID-19, and the actual start of the 2020 flight period was missed, as a local resident observed one *C. palaemon* during a casual survey before volunteers were on site.

The lack of statistically significant correlations between *N-hat* and other variables in 2019–20 suggested their daily population size estimates should be treated with caution. Based on *C. palaemon* minimum lifespans from 2019–22 (a maximum of 406 h and mean of 77.1 h), 2020 *N-hat* population peak declined too rapidly for the estimates to be considered reliable. *N-hat* and *Pmin* were not significantly correlated in 2021, however a very highly significant ρ-value and strong positive r-value between *N-hat* and *Rec* (number of records per day) ($r = 0.730$, $\rho = < 0.001$) 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. A paucity of capture-recapture data was considered responsible for unlikely estimates towards the end of the flight period.

Population estimates from the Jolly-Seber method 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 (314 and 332) signal reliability, 28 *C. palaemon* would need to have been sampled in 2019 and 30 in 2020 to reach the 9% minima. We captured 25 native English individuals (8%) in 2019, sampled the site daily (versus a mean lifespan of three days at Fineshade Wood), and know that *C. palaemon* can live for up to 17–18 days (Ravenscroft 1992) – proven by the recapture of 2201M 17 days after initial capture. Given we know 42 *C. palaemon* were released in 2018, the 2019 population would need to have increased to > 382 butterflies for model estimates to become unreliable (< 9% of the total population sampled). Although 16 *C. palaemon* were captured in 2020 (4.8% of estimate), 21 in 2021 (2.9%), and 29 in 2022 (4.9%), known population size in the 2018 reintroduction year provided a baseline against which subsequent model estimates could be tested for accuracy. Given the expected high mortality in each flight period, however, daily model estimates and captures could be used instead of gross estimates to calculate mean sampling percentages. Using this metric, 31.0% of the native English population was sampled in 2019, 18.4% in 2020, 32.5% in 2021, and 27.8% in 2022, meaning all years exceeded the 9% minima.

Conventional MRR studies have shown populations are much higher than casual observations demonstrate (e.g. Thomas 1983b; Warren 1987), however intensive sampling has proved capturing up to 50% of a population present on one day when numbers are low is possible (Brereton 1997). Sampling was intensive and regularly exceeded 16 h per day during the first two weeks of the 2021 flight period, therefore a gross population estimate of 721 appears illogical given the low encounter rate versus previous flight periods despite similarities in recapture rate. However, bearing the high mortality, mobility of the reintroduced population and, therefore, dispersal potential in mind (three butterflies were recaptured > 1 km from initial capture location), a vast majority of butterflies will not have been captured before they expired, or, in some cases, flew beyond the monitored site boundary. Two 2021 specimens were detected in woodland edge habitat > 430 m from regularly sampled ride sections.

Known occupied site area increased from 65 ha in 2019 to 87 ha by 2022. Wider dispersal is further evidenced by the increasing number of capture-recapture events on, or beyond, the periphery of the release site, on secondary or tertiary ride sections. In 2019 and 2020, only two such events occurred on secondary or tertiary ride sections. In 2021, this number rose to three, then eight in 2022 (Fig. 2). This increase cannot be explained by a corresponding change in survey effort bias on secondary rides as a proportion of overall site coverage in metres walked, which was 12.4%, 10.5%, 21.7%, and 13.2% from 2019–22. 2201M dispersed 938 m from the heart of the release site to a tertiary ride in eight days, only to be recaptured for the fourth and final time a further nine days later, a mere 240 m from the location he was first sighted at, having travelled a maximum 1,154 m between recapture events and a total distance of 2,222 m at ride-level. Given 2201M was recaptured only once over 14 days, it is plausible the butterfly flew further during this time period than the observed 2,055 m.

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 1 km or more.” He also encountered females “in situations unsuitable to support populations” several kilometres away from recognised colonies. A single female was seen flying over 6 km from a known site. Scottish females, more generally, are thought to fly > 1 km in round trips from pupal eclosion sites to nectaring, mating, and egg-laying grounds. Similarly, 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 movements recorded over one day or greater at Ariundle were 549 m for males and 197 m for females, and 410 m at Chambers Farm Wood by both sexes. However, at Fineshade Wood, using straight line measurements for accurate comparison to Scottish movements, one butterfly covered 622 m in 23 h, whilst two others covered 470 m and 950 m in 25 h.

As discussed, maximum distances travelled at Fineshade Wood were much larger still (see Fig. 5). Smaller sample size (Ravenscroft captured 66 individuals with movement data spanning one day or greater compared to our 29) but larger maximum movements at Fineshade Wood (1,630 m) compared to Ariundle (549 m) were almost certainly accounted for by our larger, but more intensively sampled survey area, as shown by our higher mean movement between captures over one day or greater (98 m for males and 79 m for females at Ariundle, and 314 m for males and 172 m for females at Fineshade Wood). Maximum duration between initial and last capture at Ariundle was 17 days (Ravenscroft 1992) – the same time period observed at Fineshade Wood during this study. Moore (2004) saw the number of marked individuals decline rapidly in Chambers Farm Wood after two days using MRR, shorter than the mean lifespan at Fineshade of three days and five hours using PMR. Based on our findings, we argue *C. palaemon* should not generally be described as sedentary, but a semisedentary species regularly capable of covering larger distances.

Validating conventional sampling methods

Although significant correlations between *N-hat* and *Pmin*, *Idx*, and *Rec* were not found for all flight periods, when 2019–22 data were combined, and 2022 analysed individually, significant correlations were found between *N-hat* and all variables (Table 1). Highly significant ($\rho = <0.01$) correlations were found between *N-hat* and *Idx* ($r = 0.559$), *Pmin* ($r = 0.563$), and *Rec* ($r = 0.557$) in 2022, whilst very highly significant ($\rho = <0.001$) correlations were found between *N-hat* and other variables when 2019–22 data were combined (*Idx* $r = 0.430$; *Pmin* $r = 0.452$; *Rec* $r = 0.501$). Positive r-values were stronger in 2022 than when 2019–22 data were combined, suggesting that 2022 data in isolation reached a quantitative threshold that surpassed 2019, 2020, and 2021 data, from which only *N-hat* was significantly correlated with *Rec* in 2021 ($r = 0.730$; $\rho = <0.001$). Significant 2019–22 and 2022 dataset correlations suggest broad agreement between daily encounter rates and daily population size estimates – a relationship weakened when pre-2022 years are analysed in isolation due to lack of quantitative data. The correlation between absolute numbers calculated (*N-hat*) and observational indices (encounter rate) therefore reaffirms the reliability of PMR in receipt of sufficient sample sizes of capture-recapture data, as well as supporting reduced effort timed counts for monitoring populations. Crucially, it also proves that simple sampling methods such as timed counts carried out at a known intensity can be used to assess the reintroduced *C. palaemon* population when the resources to coordinate PMR do not exist.

In 2022, the 29 individual *C. palaemon* captured, 14 specimens recaptured, 28 overall recaptures, and 12 observed lifespans > 24 h exceeded totals from all previous years. Accordingly, stronger, more significant correlations were found between 2022 variables than those in other years, as PMR data used to generate daily population estimates through capture-recapture histories are reliant on total captured and recaptured butterflies and cumulative recaptures distributed across a flight period. Reliable PMR data is therefore dependent on high butterfly abundance, intensive population sampling, and good site coverage to increase the number of gross recaptures, as well as the likelihood of individual butterflies being recaptured over longer time periods.

Due to both encounter rate and population index correlations with *N-hat*, we 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. When grouping the two strongest years, 2019 and 2022 (see Table 2 and Fig. 2), and excluding 2020–21 data from analysis, *Idx* and *Pmin*

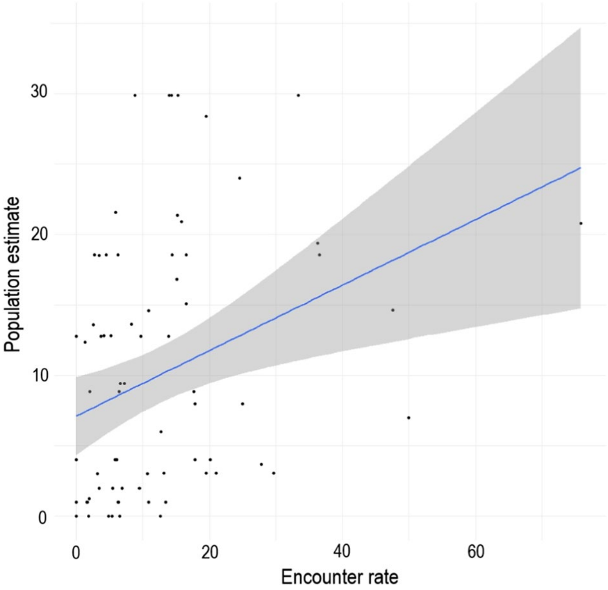


Fig. 7 Combined 2019–22 daily *C. palaemon* population estimates (*N-hat*) plotted against encounter rate per day*1000 (*Pmin*) with a linear trendline (in blue) demonstrating the linear equation $y = 0.2324(x) + 7.1083$ ($\rho = < 0.01$). A 95% upper and lower confidence interval is shown in dark grey above and below and the trendline

remained correlated with *N-hat*. However, the coefficient was slightly weakened in both cases ($r = 0.461$, $\rho < 0.01$ and $r = 0.444$, $\rho < 0.001$ for *Idx* and *Pmin*, respectively) compared to 2022 data alone. This would suggest that the threshold for quantitative sufficiency falls somewhere between 2019 and 2022's 9–14 recaptured native English individuals and 18–28 total recaptures over a single *C. palaemon* flight period. However, as 10 individuals were recaptured in 2020, we can assume the threshold for individuals is at least that. These numbers are only likely to be achieved through a combination of good emergence and high survey effort. Plotting 2019–22 daily encounter rate against population estimate data generated a linear trendline and equation of $y = 0.2324(x) + 7.1083$ (Fig. 7). This equation can be used to quickly estimate population size per day (y) in future flight periods by processing survey effort and *C. palaemon* sightings (from UKBMS monitoring forms) to generate an encounter rate (x).

Benefits of photographic mark-recapture

MRR has been used to estimate abundance for a range of Lepidoptera species (e.g. Bourn and Thomas 1993; Williams 2002; Nowicki 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 and Wedlake 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 et al. 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 baiting (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.

PMR 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 butterfly 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 et al. 1987) (Table 5).

Table 5 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 upperside wing or thoracic markings Habitat damage is likely using MRR and considered detrimental Species population density is low Species is rare, endangered, or reintroduced Capture and handling of specimens is considered an unacceptable risk A large number of volunteers with cameras are present
Mark-release-recapture (MRR)	Species has indistinct upperside wing or thoracic markings Habitat damage is unlikely or not considered detrimental Species population density is high Species is common or abundant where found Capture and handling of specimens is not considered an unacceptable risk A small number of volunteers or no volunteers are present

In the case of *C. palaemon*, 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 native 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 1,473 m away 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 which ovipositing females move through more slowly due to high resource density may increase the likelihood of fresh *C. palaemon* captures during the following flight period (e.g. Kareiva and Odell 1987; Morris and Kareiva 1991; Dover 1997; Schultz and Crone 2001; Klaassen et al. 2006; Kuefler et al. 2010).

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 *C. palaemon* through photo-identification. 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 (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). High-resolution photography has been used to identify microhabitats for grassland butterfly species in agricultural landscapes (Habel et al. 2018), whilst Interactive Individual Identification System (I^3S) Pattern photo-identification software (den Hartog and Reijns 2014) has been used to study movement patterns and dispersal barriers in Danish marsh fritillary *Euphydryas aurinia* populations. I^3S has also been used to identify two terrestrial vertebrates (Treilibs et al. 2016). 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; Genov et al. 2018; 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 AI capable of identifying individual butterflies through photographs will improve cost-efficiency of PMR sampling of *C. palaemon* and other rare and endangered Lepidoptera with unique wing markings, and enable this approach to be adopted more widely in butterfly population studies the future. 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 new colonies in England.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02837-6.

Author contributions J.P.W. wrote the main manuscript text and prepared all figures and tables. All authors reviewed the manuscript.

Funding J.P.W. was funded by the University of Northampton, Butterfly Conservation (and its Bedfordshire & Northamptonshire and Cambridgeshire & Essex Branches), the Heather Corrie Fund, and the British Entomological & Natural History Society's Maitland Emmet Research Fund.

S.O. was funded by the National Lottery Heritage Fund, Patsy Wood Trust, the UK Government's Green Recovery Challenge Fund, and supporters of Butterfly Conservation.

This study would not have been possible without the many dedicated volunteers who spent hundreds of hours recording and photographing Chequered Skipper at Fineshade Wood in Northamptonshire.

Declarations

Competing interests The authors declare no competing interests.

References

Bird CD, Hilchie GJ, Kondla NG, Pike EM, Sperling FAH (1995) Alberta butterflies. The Provincial Museum of Alberta, Edmonton

Bishop JA, Sheppard PM (1973) An evaluation of two capture-recapture models using the technique of computer simulation. In: Bartlett MS and Hiorns RW (ed) The Mathematical Theory of the Dynamics of Biological Populations. Academic Press, London, pp 235–252

Bourn NAD, Thomas JA (1993) The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. Biol Cons 63:67–74. https://doi.org/10.1016/0006-3207(93)90075-C

Brereton TM (1997) Ecology and conservation of the butterfly *Pyrgus malvae* (Grizzled Skipper) in south-east England. Unpublished PhD thesis. University of East London, London

Brussard PF (1971) Field techniques for investigations of population structure in an "ubiquitous" butterfly. J Lepid Soc 25:22–29

California Academy of Sciences and National Geographic Society (2022) Seek by iNaturalist. California Academy of Sciences and National Geographic Society, California

Collier RV (1966) Status of butterflies on Castor Hanglands, N.N.R. 1961–1965 inclusive. J Northants Natur Hist Soc and FC 35:451–456

Collier RV (1978) The status and decline of butterflies on Castor Hanglands NNR 1919-1977. Unpublished report. Nature Conservancy Council, Peterborough

Collier RV (1986) The conservation of the chequered skipper in Britain. Focus on Nature Conservation, 16. Nature Conservancy Council, Peterborough

Cooch GC, White GC (eds) (2014) Program Mark: A Gentle Introduction. 14th edition. Available at: https://www.phidot.org/software/mark/docs/book/. Accessed 30 Mar 2023

de Heer M, Kapos V, Ten Brink BJE (2005) Biodiversity trends in Europe: development and testing of a species trend indicator for evaluating progress towards the 2010 target. Philos Trans R Soc B Biol Sci 360:297–308

Dempster JP (1971) The population ecology of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae). Oecologia 7:26–67

den Hartog J, Reijns R (2014) I^{3}S Pattern manual — Interactive Individual Identification System. July 2014, version 4.0.2. Available at: https://reijns.com/wp-content/uploads/2020/01/I3S-Pattern-1.pdf. Accessed 30 Aug 2023

den Heyer CE, Bowen WD, McMillan JI (2013) Long-term changes in grey seal vital rates at Sable Island estimated from POPAN mark-resighting analysis of branded seals. Canadian Sciences Advisory Secretariat Research Document 2013/021 – Maritimes Region. Bedford Institute of Oceanography, Dartmouth, Nova Scotia

Dover JW (1997) Conservation headlands: effects on butterfly distribution and behaviour. Agric Ecosyst Environ 63:31–49

Eeles P (2019) Life Cycles of British and Irish Butterflies. Pisces Publications, Berkshire

Ehl S, Holzhauer SIJ, Ryrholm N, Schmitt T (2019) Phenology, mobility and behaviour of the arcto-alpine species *Boloria napaea* in its arctic habitat. Sci Rep 9(1):3912. https://doi.org/10.1038/s41598-019-40508-7

Ehrlich PR, Davidson SE (1960) Techniques for capture-recapture studies of Lepidoptera populations. J Lepid Soc 14:227–229

Emmet AM, Heath J (eds) (1989) The moths and butterflies of Great Britain and Ireland. Volume 7, Part 1: Hesperiidae—Nymphalidae. The Butterflies. Harley, Colchester

Farrell L (1973) A preliminary report on the status of the chequered skipper butterfly (Carterocephalus palaemon) Pall.). Unpublished report. Joint Committee for the Conservation of British Insects and World Wildlife Fund, Huntingdon

Fearnbach H, Durban J, Parsons K, Claridge D (2012) Photographic mark–recapture analysis of local dynamics within an open population of dolphins. Ecol Appl 22(5):1689–1700

Field Studies Council (2022) FSC QGIS TomBio tools plugin for biological recorders, Version 3.4.1. Available at: https://www.fscbiodiversity.uk/fsc-plugin-qgis-v3. Accessed 4 Oct 2023

Fletcher J (1899) Notes on the preparatory stages of *Carterocephalus mandan*. Can Entomol 21:113–116

Fox R, Dennis E, Purdy K, Middlebrook I, Roy DB, Noble D, Botham M, Bourn N (2023) The State of the UK's Butterflies 2022. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham, Dorset

Franzén M, Nilsson SG, Johansson V, Ranius T (2013) Population fluctuations and synchrony of grassland butterflies in relation to species traits. Plos One 8(10):e78233. https://doi.org/10.1371/journal.pone.0078233

Fric Z, Konvička M (2007) Dispersal kernels of butterflies: Power-law functions are invariant to marking frequency. Basic Appl Ecol 8(4):377–386. https://doi.org/10.1016/j.baae.2006.06.005

Frohawk FW (1892) Life-history of *Carterocephalus palaemon*. Entomologist 25: 225–228, 254–256

Frohawk FW (1934) The complete book of British butterflies. Ward, Lock and Company, London

Gailey G, Karczmarski L (2012) DISCOVERY: Photo-identification data-management system for individually recognizable animals. Available at: http://www.biosch.hku.hk/ecology/staffhp/lk/Discovery/index.html. Accessed 15 Oct 2022

Gall LF (1984) The effect of capturing and marking on subsequent activity in *Boloria acrocnema* (Lepidoptera: Nymphalidae), with a comparison of different numerical models that estimate population size. Biol Cons 28:139–154

Galletti Vernazzani B, Jackson JA, Cabrera E, Carlson CA, Brownell RL (2017) Estimates of abundance and trend of Chilean blue whales off Isla de Chiloe, Chile. Plos ONE 12(1):e0168646. https://doi.org/10.1371/journal.pone.0168646

Genov T, Centrih T, Wright AJ, Wu G-M (2018) Novel methods for identifying individual cetaceans using facial features and symmetry: A test case using dolphins. Mar Mamm Sci 34:514–528. https://doi.org/10.1111/mms.12451

Google LLC (2022) Google Lens. Google LLC., California

Gore MA, Frey PH, Ormond RF, Allan H, Gilkes G (2016) Use of Photo-identification and mark-recapture methodology to assess basking shark (*Cetorhinus maximus*) Populations. PLoS ONE 11(3): e0150160. https://doi.org/10.1371/journal.pone.0150160

Haahtela T, Saarinen K, Ojalainen P, Aarnio H (2011) Butterflies of Britain and Europe: a photographic guide. A and C Black, London

Habel JC, Teucher M, Rödder D (2018) Mark-release-recapture meets Species Distribution Models: Identifying micro-habitats of grassland butterflies in agricultural landscapes. PLoS ONE 13(11):e0207052. https://doi.org/10.1371/journal.pone.0207052

Haddad NM, Hudgens B, Damiani C, Gross K, Kuefler D, Pollock K (2008) Determining optimal population monitoring for rare butterflies. Conserv Biol 22(4):929–940

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12(10):e0185809. https://doi.org/10.1371/journal.pone.0185809

Higgins ND, Riley LG (1983) A field guide to the butterflies of Britain and Europe. 5th edition. Harper-Collins, London

Hinneberg H, Döring J, Hermann G, Markl G, Theobald J, Aust I, Bamann T, Bertscheit R, Budach D, Niedermayer J, Rissi A, Gottschalk TK (2022) Multi-surveyor capture-mark-recapture as a powerful tool for butterfly population monitoring in the pre-imaginal stage. Ecol Evol 12(8):e9140. https://doi.org/10.1002/ece3.9140

Hinneberg H, Kőrösi Á, Gottschalk T (2023) Providing evidence for the conservation of a rare forest butterfly: results from a three-year capture-mark-recapture study. Basic Appl Ecol. https://doi.org/10.1016/j.baae.2023.09.001

IBM Corporation (2021) IBM SPSS Statistics for Windows (version 28.0). Armonk, New York

Junker M, Schmitt T (2010) Demography, dispersal and movement pattern *of Euphydryas aurinia* (Lepidoptera: Nymphalidae) at the Iberian Peninsula: an alarming example in an increasingly fragmented landscape? J Insect Conserv 14(3):237–246. https://doi.org/10.1007/s10841-009-9250-1

Kareiva P, Odell G (1987) Swarms of predators exhibit prey taxis if individual predators use area-restricted search. Am Nat 130:233–270

Klaassen RHG, Nolet BA, Bankert D (2006) Movement of foraging tundra swans explained by spatial pattern in cryptic food densities. Ecology 87:2244–2254

Kuefler D, Hudgens B, Haddad NM, Morris WF, Thurgate N (2010) The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology 91:944–950

Lamb HF (1974) The chequered skipper Carterocephalus palaemon (Pallas) field survey. Unpublished report. Institute of Terrestrial Ecology and Joint Committee for the Conservation of British Insects, Huntingdon

LeCun Y, Bengio Y, Hinton G (2015) Deep learning. Nature 521:436–444. https://doi.org/10.1038/nature14539

Lewis OT, Thomas CD, Hill JK, Brookes MI, Robin Crane TP, Graneau YA, Mallet JLB, Rose OC (1997) Three ways of assessing metapopulation structure in the butterfly *Plebejus argus*. Ecological Entomology 22:283–293. https://doi.org/10.1046/j.1365-2311.1997.00074.x

Mallet J (1986) Dispersal and gene flow in a butterfly with home range behaviour: *Heliconius erato* (Lepidoptera: Nymphalidae). Oecologia 68:210–217

Mallet J, Longino T, Murawski D, Murawski A, Simpson De Gambao A (1987) Handling effects in Heliconius: where do all the butterflies go? J Anim Ecol 56:377–386

Mazzoil M, McCulloch SD, Defran R, Titcomb EM (2004) Use of digital photography and analysis of dorsal fins for photo identification of Bottlenose Dolphins. Aquat Mamm 30(2):209–219

Microsoft Corporation (2021) Microsoft Excel. Available at: https://office.microsoft.com/excel. Accessed 17 Mar 2024

Molls C (2021) The Obs-Services and their potentials for biodiversity data assessments with a test of the current reliability of photo-identification of Coleoptera in the field. Tijdschr Entomol 164:143–153

Moore JL (2004) The ecology and re-introduction of the chequered skipper butterfly Carterocephalus palaemon in England. Unpublished PhD thesis. University of Birmingham, Birmingham

Morris WF, Kareiva PM (1991) How insect herbivores find suitable host plants: the interplay between random movement and nonrandom movement. In: Bernays E (ed) Insect-Plant Interactions. CRC Press, Boston, pp 176–208.

Morton AC (1982) The effects of marking and capture on recapture frequencies of butterflies. Oecologia 53(1):105–110

Morton AC (1984) The effect of marking and handling on recapture frequencies of butterflies. In: Vane-Wright RI, Ackery PR (eds) The Biology of Butterflies. Academic Press, London, pp 55–58

Murphy DD, Menninger MS, Ehrlich PR, Wilcox BA (1986) Local population dynamics of adult butterflies and the conservation status of two closely related species. Biol Cons 37(3):201–223. https://doi.org/10.1016/0006-3207(86)90082-0

Nowicki P (2017) Survey precision moderates the relationship between population size and stability. Biol Cons 212:310–315. https://doi.org/10.1016/j.biocon.2017.06.04

Nowicki P, Witek M, Skórka P, Settele J, Woyciechowski M (2005) Population ecology of the endangered butterflies *Maculinea teleius* and *M. nausithous* and the implications for conservation. Popul Ecol 47:193–202

Nowicki P, Settele J, Henry P, Woyciechowski M (2008) Butterfly monitoring methods: the ideal and the real world. Israel J Ecol Evol 54(1):69–88. https://doi.org/10.1560/IJEE.54.1.69

Observation International (2022) ObsIdentify. Observation International, Aarlanderveen

Pennekamp F, Garcia-Pereira P, Schmitt T (2014) Habitat requirements and dispersal ability of the Spanish Fritillary (*Euphydryas desfontainii*) in southern Portugal: evidence-based conservation suggestions for an endangered taxon. J Insect Conserv 18(3):497–508. https://doi.org/10.1007/s10841-014-9655-3

Peterken GF (1976) Long-term changes in the woodlands of the Rockingham Forest and other areas. J Ecol 64:123–146

Peterken GF, Harding PT (1974) Recent changes in the conservation value of woodlands in Rockingham Forest. For Int J For Res 47(2):109–128

Pollard E (1977) A method for assessing changes in the abundance of butterflies. Biol Cons 12:115–134

Pollard E (1982) Monitoring butterfly abundance in relation to the management of a nature reserve. Biol Cons 24:317–328

Prusa LA, Hill RI (2021) Umbrella of protection: spatial and temporal dynamics in a temperate butterfly Batesian mimicry system. Biol J Lin Soc 133(3):685–703. https://doi.org/10.1093/biolinnean/blab004

QGIS Development Team (2021) QGIS geographic information system. Open Source Geospatial Foundation. Available at: https://qgis.osgeo.org. Accessed 17 Mar 2024

R Core Team (2024) R: A Language and Environment for Statistical Computing, Version 4.3.3. R Foundation for Statistical Computing, Vienna, Austria

Rákosy L, Schmitt T (2011) Are butterflies and moths suitable ecological indicator systems for restoration measures of semi-natural calcareous grassland habitats? Ecol Ind 11(5):1040–1045. https://doi.org/10.1016/j.ecolind.2010.10.010

Ravenscroft NOM, Warren MS (1992) Habitat selection by larvae of the chequered skipper butterfly, *Carterocephalus palaemon* (Pallas) (Lepidoptera: Hesperiidae) in Northern Europe. Entomol Gaz 43:237–242

Ravenscroft NOM (1991) The habitats of the larvae of the chequered skipper Carterocephalus palaemon in northern Europe. Unpublished report. British Butterfly Conservation Society, Wareham

Ravenscroft NOM (1992) The ecology and conservation of the chequered skipper butterfly Carterocephalus palaemon (Pallas). Unpublished PhD thesis. University of Aberdeen, Aberdeen

Ravenscroft NOM (1995) The conservation of Carterocephalus palaemon in Scotland. In: Pullin AS (ed) Ecology and conservation of butterflies. Chapman and Hall, London, pp 165-179

Roland J, Keyghobadi N, Fownes S (2000) Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology 81:1642–1653. https://doi.org/10.1890/0012-9658(2000)081[1642:apbdeo]2.0.CO;2

Rollason WA (1908) Life-history of *Hesperia paniscus*, F., *palaemon*. Pallas; Staud Cat Entomologist 41:102–106

Rosel PE, Mullin KD, Garrison L, Schwacke L, Adams J, Balmer B, Conn P, Conroy MJ, Eguchi T, Gorgone A, Hohn A, Mazzoil M, Schwartz C, Sinclair C, Speakman T, Urian K, Vollmer N, Wade P, Wells R, Zolman E (2011) Photo-identification Capture-Mark-Recapture Techniques for Estimating Abundance of Bay, Sound and Estuary Populations of Bottlenose Dolphins along the US East Coast and Gulf of Mexico: A Workshop Report. NOAA Technical Memorandum NMFS-SEFSC-621. US Department of Commerce, Lafayette, Los Angeles

Ruiz de la Hermosa A, Truyols-Henares F, Pinya S (2022) Individual photographic identification based on unique colour pattern of the thorax of *Acherontia atropos* (Linnaeus, 1758) (Lepidoptera: Sphingidae). SHILAP Rev Lepidopterol 50:33–41

Schtickzelle N, Le Boulengé E, Baguette M (2002) Metapopulation dynamics of the bog fritillary butterfly: demographic processes in a patchy population. Oikos 97(3):349–360. https://doi.org/10.1034/j.1600-0706.2002.970305.x

Schultz CB, Crone EE (2001) Edge-mediated dispersal behavior in a prairie butterfly. Ecology 82:1879–1892

Schwarz CJ, Arnason AN (1996) A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860–873

Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze ED, Vogt J, Wöllauer S, Weisser WW (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574:671–674. https://doi.org/10.1038/s41586-019-1684-3

Sielezniew M, Deoniziak K, Dziekańska I, Nowicki P (2019) Dispersal in a metapopulation of the critically endangered Danube Clouded Yellow butterfly *Colias myrmidone*: implications for conservation. J Insect Conserv 23(2):291–300. https://doi.org/10.1007/s10841-019-00126-0

Singer MC, Wedlake P (1981) Capture does affect probability of recapture in a butterfly species. Ecol Entomol 6:215–216

Skylum Software (2020) Luminar, version 4.3.4 (9699). Skylum Software, New York

Southwood TRE and Henderson PA (2000) Ecological Methods. Blackwell Science, London

Taron D, Ries L (2015) Butterfly monitoring for conservation. In: Daniels J (ed) Butterfly conservation in North America. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9852-5_3

Thomas JA (1983a) A quick method for estimating butterfly numbers during surveys. Biol Cons 27:195–211

Thomas JA (1983b) The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. J Appl Ecol 20(1):59–83

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philos Trans R Soc B Biol Sci 360:339–357. https://doi.org/10.1098/rstb.2004.1585

Thomas JA, Lewington R (2016) The Butterflies of Britain and Ireland – new revised edition. Bloomsbury, London

Thompson JW, Zero VH, Schwacke LH, Speakman TR, Quigley BM, Morey JSM, McDonald TL (2019) finFindR: Computer-assisted Recognition and Identification of Bottlenose Dolphin Photos in R. Preprint. https://doi.org/10.1101/825661v1.full

Tolman T, Lewington R (2008) Collins butterfly guide: the most complete field guide to the butterflies of Britain and Europe. 2nd edition. HarperCollins, London

Treilibs C, Pavey C, Hutchinson M, Bull C (2016) Photographic identification of individuals of a free-ranging, small terrestrial vertebrate. Ecol Evol 6:800–808. https://doi.org/10.1002/ece3.1883

Tubbs SE, Baş AA, Côté G, Jones AL, Notman G (2019) Sighting and stranding reports of Irrawaddy dolphins (*Orcaella brevirostris*) and Dugongs (*Dugong dugon*) in Kep and Kampot, Cambodia. Aquatic Mammals 45(5):563–568

Turlure C, Pe'er G, Baguette M, Schtickzelle N (2017) A simplified mark–release–recapture protocol to improve the cost effectiveness of repeated population size quantification. Methods Ecol Evol 9:645–656. https://doi.org/10.1111/2041-210X.12900

UK Centre for Ecology and Hydrology (2022a) iRecord, Version 6.1.0. UK Centre for Ecology and Hydrology, Oxfordshire, England. Available at: https://irecord.org.uk/app. Accessed 02 Apr 2024

UK Centre for Ecology and Hydrology (2022b) iRecord Butterflies, Version 2.5.4. UK Centre for Ecology and Hydrology, Oxfordshire, England. Available at: https://www.brc.ac.uk/app/irecord-butterflies. Accessed 02 Apr 2024

Ulrich W, Schmitt T, Gros P, Trusch R, Habel JC (2023) Synchronous long-term trends in abundance and compositional variability of butterflies in Central Europe. Ecosphere 14(7):e4615. https://doi.org/10.1002/ecs2.4615

van Swaay CAM, Warren MS (2012) Developing butterflies as indicators in Europe: current situation and future option*s*. De Vlinderstichting/Dutch Butterfly Conservation, Butterfly Conservation UK, Butterfly Conservation Europe, Wageningen, Netherlands

van Swaay CAM, Regan E, Ling M, Bozhinovska E, Fernandez M, Marini-Filho OJ, Huertas B, Phon, C-K, Korösi A, Meerman J, Pe'er G, Uehara-Prado M, Sáfián S, Sam L, Shuey J, Taron D, Terblanche R, Underhill L (2015) Guidelines for Standardised Global Butterfly Monitoring. GEO BON Technical Series 1. Group on Earth Observations Biodiversity Observation Network, Leipzig, Germany

van Swaay CAM, Dennis EB, Schmucki R, Sevilleja CG, Balalaikins M, Botham M, Bourn N, Brereton T, Cancela JP, Carlisle B, Chambers P, Collins S, Dopagne C, Escobés R, Feldmann R, Fernández-García JM, Fontaine B, Gracianteparaluceta A, Harrower C, Harpke A, Heliölä J, Komac B, Kühn E, Lang A, Maes D, Mestdagh X, Middlebrook I, Monasterio Y, Munguira ML, Murray TE, Musche M, Õunap E, Paramo F, Pettersson LB, Piqueray J, Settele J, Stefanescu C, Švitra G, Tiitsaar A, Verovnik R, Warren MS, Wynhoff I, Roy DB (2019) The EU Butterfly Indicator for Grassland species: 1990–2017: Technical Report. Butterfly Conservation Europe & ABLE/eBMS

van Swaay CAM, Dennis EB, Schmucki R, Sevilleja CG, Aghababyan K, Åström S, Balalaikins M, Bonelli S, Botham M, Bourn NAD, Brereton TM, Cancela JP, Carlisle B, Chambers P, Collins S, Dopagne C, Dziekanska I, Escobés R, Faltynek Fric Z, Feldmann R, Fernández-García JM, Fontaine B, Goloshchapova S, Gracianteparaluceta A, Harpke A, Harrower C, Heliölä J, Khanamirian G, Kolev Z, Komac B, Krenn H, Kühn E, Lang A, Leopold P, Lysaght L, Maes D, McGowan D, Mestdagh X, Middlebrook I, Monasterio Y, Monteiro E, Munguira ML, Musche M, Õunap

E, Ozden O, Paramo F, Pavlíčko A, Pettersson LB, Piqueray J, Prokofev I, Rákosy L, Roth T, Rüdisser J, Šašić M, Settele J, Sielezniew M, Stefanescu C, Švitra G, Szabadfalvi A, Teixeira SM, Tiitsaar A, Tzirkalli E, Verovnik R, Warren MS, Wynhoff I, Roy DB (2020) Assessing Butterflies in Europe - Butterfly Indicators 1990- 2018 Technical report. Butterfly Conservation Europe and ABLE/eBMS

Vlasanek P, Sam L, Novotny V (2013) Dispersal of butterflies in a New Guinea rainforest: using mark–recapture methods in a large, homogeneous habitat. Ecol Entomol 38:560–569

Wagner DL, Fox R, Salcido DM, Dyer LA (2021) A window to the world of global insect declines: moth biodiversity trends are complex and heterogeneous. Proc Natl Acad Sci 118:e2002549117. https://doi.org/10.1073/pnas.2002549117

Warren MS (1987) The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. J Appl Ecol 24:483–498

Warren MS (1990) The Chequered Skipper Carterocephalus palaemon in Northern Europe. The British Butterfly Conservation Society Limited, Chequered Skipper Working Party, Dorchester, Dorset

Warren MS (1995) Managing local micro-climates for the High Brown Fritillary, *Argynnis adippe*. In: Pullin AS (ed) Ecology and conservation of butterflies. Chapman & Hall, London, pp 198-210

Weidemann HJ (1988) Tagfalter (Band 2): Biologie, Ökologie, Biotopschutz. Neuman-Neudamm, Germany

Wepprich T, Adrion JR, Ries L, Wiedmann J, Haddad NM (2019) Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. PLoS ONE 14(7):e0216270. https://doi.org/10.1371/journal.pone.0216270

Weyer J, Schmitt T (2013) Knowing the way home: strong philopatry of a highly mobile insect species, *Brenthis ino*. J Insect Conserv 17(6):1197–1208. https://doi.org/10.1007/s10841-013-9601-9

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46(supplement):s120-139

Wildman JP, Ollerton J, Bourn NAD, Brereton TM, Moore JL, McCollin D (2022) The value of museum and other uncollated data in reconstructing the decline of the chequered Jamie P. Wildman – May 2023 178 skipper butterfly *Carterocephalus palaemon* (Pallas, 1771). J Nat Sci Collect 10:31–44

Wildman JP (2023) The History, Ecology, and Reintroduction of the Chequered Skipper Butterfly Carterocephalus palaemon in England. Unpublished PhD thesis. University of Northampton, Northampton

Williams AAE, Coppen, RAM, Williams MR (2018) A method for conducting mark-release-recapture studies of the graceful sun-moth *Synemon gratiosa* (Lepidoptera: Castniidae). Rec West Aust Mus 33(2):181–186. https://doi.org/10.18195/issn.0312-3162.33(2).2018.181-186

Williams MR (2002) Effect of fire on day-flying Lepidoptera in Koondoola Bushland reserve. Progress Report 1. Department of Conservation and Land Management and Curtin University of Technology, Western Australia

Wilson RJ, de Siqueira AF, Brooks SJ, Price BW, Simon LM, van der Walt SJ, Fenberg PB (2022) Applying computer vision to digitised natural history collections for climate change research: Temperature-size responses in British butterflies. Methods Ecol Evol 00:1–13. https://doi.org/10.1111/2041-210X.13844

Wood H (1908) Notes on the life-history of *Cyclopides palaemon*. Entomol Rec 20:65–66

Zeng Q, Lin W, Dai Y, Zhong M, Wang X, Zhu Q (2020) Modeling demographic parameters of an edge-of-range population of Indo-Pacific humpback dolphin in Xiamen Bay, China. Reg Stud Mar Sci 40:101462. https://doi.org/10.1016/j.rsma.2020.101462