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Providing evidence for the conservation of a rare forest butterfly: Results from a three-year capture-mark-recapture study

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ABSTRACT

Species living in spatially structured populations require a network of interconnected habitat patches. Due to changes in forest management, this network of habitat patches has been lost for insect species inhabiting open spots within forests. We studied two of the last populations of the Southern White Admiral (*Limenitis reducta*) in Germany. The aim of our study was to provide information for the conservation of this species. We conducted a capture-mark-recapture study over three consecutive years and we estimated population sizes and demographic parameters using Jolly-Seber and Cormack-Jolly-Seber models. Furthermore, we used different dispersal kernels to study the dispersal of *L. reducta*. We found that apparent survival rates differed greatly between the sexes. The mean residence times were eight to nine days for males and only two to four days for females. Apparent survival rates of both sexes decreased with increasing wing deterioration. Total population sizes of *L. reducta* varied between sites and years and ranged between 61 and 123. Daily abundances were generally low, especially that of females. The mean dispersal distance of individual recaptured butterflies increased in years with higher population densities, suggesting density-dependent dispersal. The dispersal data in our study was clearly bimodal, probably reflecting 'routine movement' at short distances and 'displacement movement' between habitat patches at longer distances. Consequently, the processes generating the dispersal data were better represented by the lognormal mixture model than by the negative exponential and the inverse power function. The mixed kernel predicted that about 9 % of the population disperses over > 1 km but that long-distance dispersal is rare. Our study highlights the urgent need for conservation measures to protect *L. reducta* in Germany and, based on our data, we recommend to create new habitat patches at distances of 1 to 1.5 km from existing habitats.

Introduction

Declining local abundance, often caused by habitat shrinkage or degradation (Bergman 2001; Mortelliti et al. 2010; Österling et al. 2010; Tilman et al. 1994; Warren et al. 2021), and decreasing connectivity of populations (Cooper & Walters 2002; Haddad et al. 2015; Krauss et al. 2010) are important mechanisms explaining species loss at the regional scale. Taken together, the decline in the local population sizes and the decreasing frequency of realised dispersal between populations are drastically affecting the dynamics of spatially structured populations (SSPs; e.g. Reed 2004). This is worrying, because many plant and animal species live in SSPs and numerous studies have shown that viable SSPs are key to the conservation of species (e.g. Cheeseman et al. 2019; Hanski & Thomas 1994; Hula et al. 2004; Rhoads et al. 2017; Stevens & Baguette 2008). SSPs are characterised by a number of subpopulations

inhabiting discrete habitat patches, loosely connected through individuals moving between the patches. SSPs with frequent movement between patches are termed 'patchy populations', those with infrequent between-patch movement and considerable turnover, i.e. local extinction and recolonization, are classical metapopulations (Harrison 1991; Ovaskainen & Hanski 2004). As the connectivity of subpopulations decreases over time, a patchy population can become a metapopulation and eventually a set of isolated populations at increased risk of extinction (e.g. Griffiths & Williams 2000).

Many butterfly species live in SSPs (e.g. Mousson et al. 1999; Ojanen et al. 2013; Örvössy et al. 2013; Wahlberg et al. 2002), among them some typical forest species (e.g. Konvička et al. 2008; Välimäki & Itämies 2003). Most forest butterflies require habitats with a high solar irradiation, e.g. clearings, glades, or ride edges (Bergman et al. 2020; Hermann 2021). Due to the loss of megaherbivores in the past and the

more recent abandonment of coppicing and clear-cutting, such open habitats in forests have drastically decreased (Hilmers et al. 2018; Kowalczyk et al. 2021; Müllerová et al. 2014; Vera 2002). As a result, habitat specialists of open forests have declined across Europe and in some regions have become extinct (Konvička & Kuras 1999; Sielezniew et al. 2019; Streitberger et al. 2012; Warren et al. 2021). Today, conservation efforts are needed to halt the loss of these species. Information on population sizes, connectivity patterns, and vital rates under different environmental conditions is essential for an evidence-based conservation but is unfortunately rarely available.

Capture-mark-recapture (CMR) experiments are one possibility to estimate demographic parameters of butterfly populations (e.g. Birch et al. 2021; Junker & Schmitt 2010; Pennekamp et al. 2014; Sielezniew et al. 2020). The application of CMR requires a certain number of re-captures and is therefore difficult for elusive or extremely rare species. However, when sufficient data can be collected, CMR studies are a valuable source of information to guide species conservation (e.g. Schtickzelle et al. 2005). Traditional Cormack-Jolly-Seber (CJS) models estimate two parameters for a population of marked animals, specifically their apparent survival rate (φ) and recapture probability (p). CJS models allow testing for differences in the two parameters between groups (e.g. sexes), with time, or in correlation with environmental or individual covariates. Jolly-Seber (JS) models are an extension of CJS models and provide estimates of abundance in addition to φ and p. Both models assume open populations, i.e. births, deaths, and permanent immigration/emigration can occur without biasing the parameter estimates. Nevertheless, CJS and JS models make two important assumptions: that sampling events are instantaneous compared with the duration of the study, and that marks are permanent.

Previous studies have shown that demographic parameters can differ greatly between the two sexes, and that the daily survival of adult butterflies can be age-dependent when nectar intake cannot compensate for the energy depletion associated with butterfly activity (Osváth-Ferencz et al. 2017; Sielezniew et al. 2020). Furthermore, weather conditions may directly or indirectly affect the survival of adult butterflies because warm and sunny conditions may trigger higher flight activity (Franzén et al. 2022; Gibbs & van Dyck 2010; Kuussaari et al. 2016), which in turn implies higher predation risk (Molleman et al. 2020), faster wing deterioration, and higher metabolic rate, which is probably associated with a faster depletion of energy reserves (Brakefield 1982; Niitepõld 2010). Consequently, incorporating individual-specific covariates and weather data into CJS models can reveal drivers of butterfly aging and help to improve model estimates.

In combination with spatial information, recaptures of marked butterflies provide valuable information on the dispersal of individuals (e.g. Fric et al. 2010; Weyer & Schmitt 2013). Various metrics have been used to describe the movements of recaptured butterflies, such as individual distances between consecutive capture locations (Ehl et al. 2019; Pennekamp et al. 2014), cumulative route distances (Fric & Konvička 2007; Junker & Schmitt 2010; Weyer & Schmitt 2013), or the largest net displacement (LND; Weyer & Schmitt 2013). The LND, i.e. the maximum Euclidean distance between a pair of capture locations of the same individual, appears to be the most relevant for describing the dispersal of butterfly populations and guiding conservation planning. The inverse power function (IPF) and the negative exponential function (NEF) are the most popular models to describe butterfly dispersal by means of mathematical functions, so-called 'dispersal distance kernels' (Fric & Konvička 2007; Nathan et al. 2012; Stevens et al. 2010). Due to self-similarity, the IPF is invariant to marking frequency and has therefore been recommended for small datasets (Fric & Konvička 2007). Unfortunately, the IPF and NEF cannot distinguish between different behavioural types of movement, such as 'routine movement' and 'displacement movement' (Van Dyck & Baguette 2005). Routine movement describes various daily activities, e.g. foraging, mate-location, locating shelters/perches/resting places. Displacement movement, on the other hand, is specifically "designed for net

displacement and settlement at some distance from the previous or natal site" (Van Dyck & Baguette 2005). Both types of movement contribute to the dispersal of individuals and thus to the dispersal kernel of populations (Hovestadt et al. 2011; Nathan et al. 2012). The contribution of each type of movement to total dispersal can vary between species and habitats, and even between years for the same population under variable weather conditions and local abundances (e.g. Bergerot et al. 2012; Cormont et al. 2011; Van Dyck & Baguette 2005; Kuussaari et al. 2016). Mixture distributions, in contrast to simplistic functions such as the IPF and NEF, can deal with the complexity of the dispersal process and offer the possibility to specifically account for the different types of butterfly movement (Hovestadt et al. 2011; Nathan et al. 2012).

The CMR methodology has been applied extensively to butterfly species with relatively high local abundance (e.g. Junker & Schmitt 2010; Weyer & Schmitt 2013). Many CMR studies have been conducted over only one flight season (but see e.g. Schtickzelle et al. 2002) and are therefore limited in their significance, as butterfly populations are subject to large inter-annual fluctuations (Franzén et al. 2013; Nowicki 2017). In our study, we recorded population sizes and dispersal distances of a low-density species at two different study sites and over three consecutive years.

The Southern White Admiral (*Limenitis reducta* Staudinger, 1901; Fig. 1) is distributed from eastern Turkey to western France (Fig. 2). It is widespread and relatively common in the Mediterranean region, but often in low densities (e.g. Hesselbarth et al. 1995; Kudrna 2002; Stefanescu & Jubany 2002). In Central Europe, the species has faced a strong decline since the first half of the 20th century. It is endangered in Austria (Höttinger & Pennerstorfer 2005), Switzerland (Wermeille et al. 2014), several French regions (MNHN & OFB 2023), and has even gone extinct in the Czech Republic (Šumpich & Liška 2018). In Germany, *L. reducta* has formerly been relatively widespread in the south but is now close to extinction, with a few remaining strongholds in the Swabian Jura (Reinhardt & Bolz 2011; Reinhardt et al. 2020). The sharp decline of *L. reducta* during the late 20th and early 21st century is probably related to changes in forest management, i.e. the abandonment of coppicing and clear-cutting. In its last German habitats, the species is associated with storm throws and forest clearings, where the host plant, Fly Honeysuckle (*Lonicera xylosteum*), grows in sunny locations. During larval hibernation, typical densities are less than three individuals per 100 m^2 of larval habitat (Hinneberg et al. 2022).

The main goals of our study were to estimate population sizes and dispersal distances of adult *L. reducta* to provide a scientific basis for conservation planning. Furthermore, we were interested in the effects of weather conditions, wing wear, and individual age on the survival of both males and females. We hypothesized that apparent daily survival would decrease during periods of favourable weather conditions (no rain, warm temperatures), as higher butterfly flight activity on these days could imply a higher risk of predation and higher metabolic rate. We also hypothesized that daily survival would decrease with increasing age and wing wear of butterflies, especially in males due to their energy-consuming behaviour of defending territories.

Materials and methods

Study species and study area

We studied two distinct populations of the nymphalid butterfly *Limenitis reducta* in its last German strongholds in the Swabian Jura. The flight period usually lasts from mid/late June to late July/early August (Hinneberg et al. 2022). While the larvae of *L. reducta* in the Swabian Jura are monophagous, feeding on the leaves of sun-exposed *L. xylosteum*, adults visit a wide range of nectaring plants with a certain preference for white-flowered umbellifers, in particular Ground Elder (*Aegopodium podagraria*). The nectaring plants are often found along forest roads (Fig. 1).

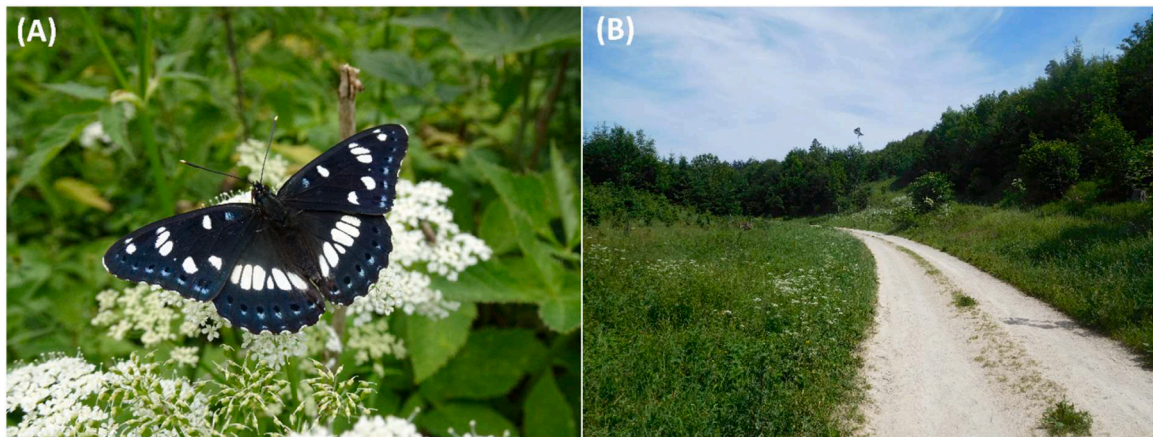The two study sites were located at the head of gently incised valleys

Fig. 1. (A) Male *Limenitis reducta* on its preferred nectar plant, *Aegopodium podagraria*. (B) Typical study transect, a sun-exposed forest road, lined with nectaring habitat.
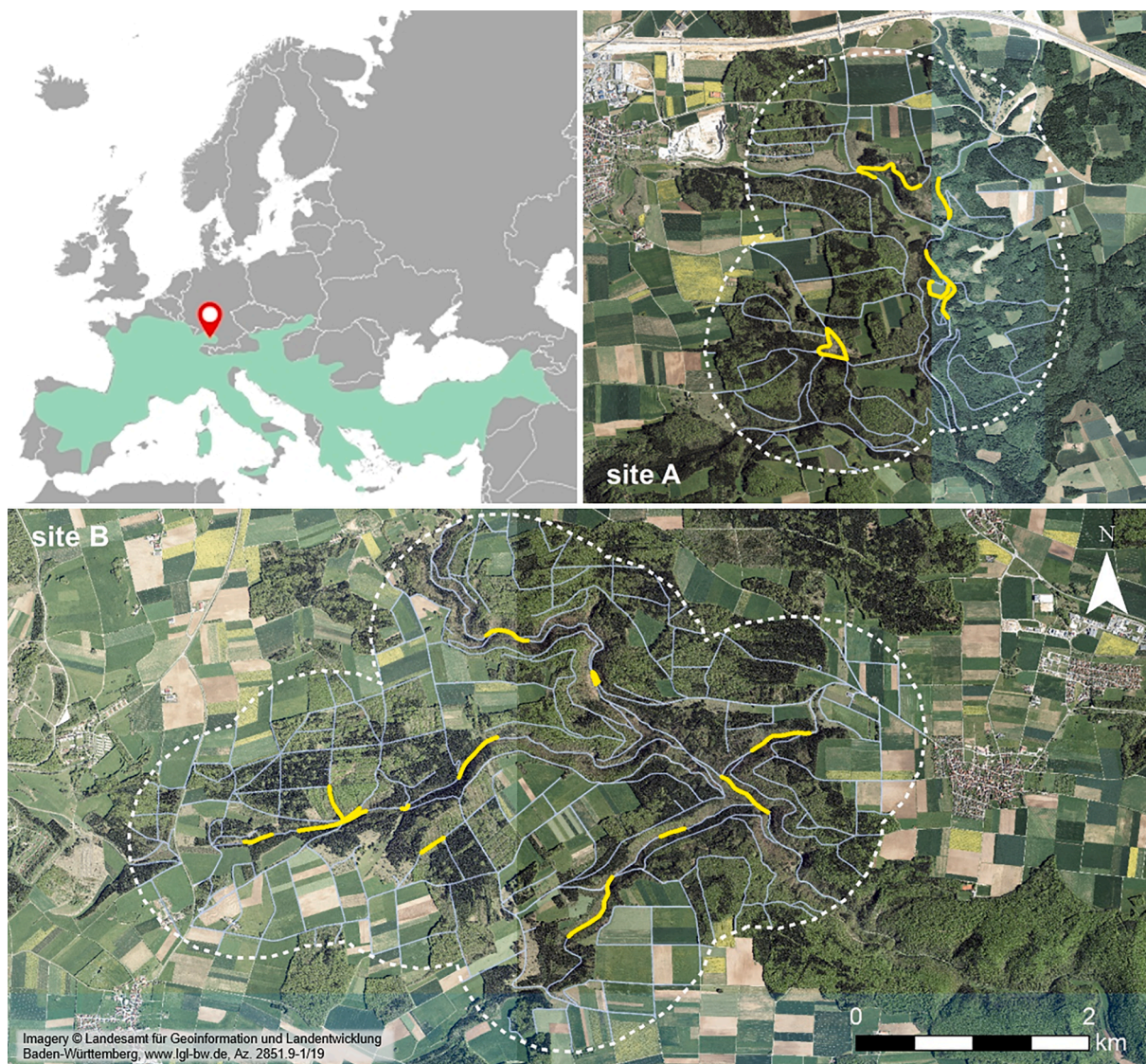

Fig. 2. Approximate distribution of *L. reducta* according to LepiDiv 2017 and location of the study sites in southwest Germany. Solid yellow lines indicate transects sampled in 2020. Dashed lines represent the boundaries of the study sites, approximated by a buffer of 1 km around the transects. Study sites A and B cover approximately 9.1 km², and 19.6 km², respectively. Thin blue lines indicate forest roads within the study sites. Note that only forest roads with wide edges and suitable nectaring habitat for *L. reducta* were selected for transects. Although *L. reducta* appears to move preferably along forest edges and forest roads, the species is also able to cross high forest stands (own observations).

at the southern edge of the Swabian Jura near Merklingen (site A, 630 – 680 m a.s.l., approximate size of the study area: 9.1 km^2) and Blaubeuren (site B, 590 – 750 m a.s.l., approximate size of the study area: 19.6 km^2). Both sites were characterised by a high forest cover (coniferous and deciduous trees), interspersed with a few older storm throws (> 20 years), clearings, small heathlands/meadows/agricultural fields, and a dense network of forest roads (Fig. 2).

Butterfly sampling

For three consecutive years, the CMR studies at both sites were mainly conducted by the first author, supported by TG and four assistants during the peak flight season. Using butterfly nets, we captured all detected adults of *L. reducta* along forest roads with adjacent nectar plants or larval habitat. The spatial arrangement of our study transects was fixed within years but varied slightly between years due to shifts in nectar plant availability. In each year, the transects covered all major nectaring habitats within the study sites. The average walking speed on the transects was 900 m/h. Total transect lengths were approximately 3.3 km and 4.9 km for sites A and B, respectively. Capturing of butterflies began when the first individual of the year was sighted, and systematic surveys ended when the number of captured individuals had gradually decreased to zero. Surveys were carried out between 10:00 a.m. and 5:00 p.m. only on days with suitable weather conditions for butterfly surveys, i.e. no rain and no dense cloud cover. All transects of site A were sampled on the same day, except in a few cases when weather conditions did not allow all transects to be visited. Sampling all transects of site B on the same day was not always possible due to the longer total length of the transects.

Using a waterproof pen (e.g. STABILO OHPen universal F), each captured *L. reducta* was marked with a unique number on the underside of the hind wings. For each captured individual, we recorded sex, wing wear, and whether it was a first capture or a recapture. We used a scale of 1.00 ('fresh') to 4.00 ('heavily worn') with increments of 0.25 to rate wing wear. Wing wear is often used as a proxy for butterfly age (e.g. Stjernholm et al. 2005), because wings cannot be repaired and hence wing damage can only increase during lifetime. The location of capture was recorded using a handheld GPS device (Garmin Oregon 700). Immediately after data collection, the butterflies were released at the place of capture. Recaptures on the same day were included in the dispersal analyses, but not in the estimation of demographic parameters and population sizes.

Recording of weather data

For 2019, we obtained weather data from the German Weather Service (station Merklingen, ID 2814, German Weather Service 2022). In 2020 and 2021, we measured temperature and dew point using USB500-data loggers (Measurement Computing Corporation) and obtained precipitation data from the German Weather Service. A self-constructed radiation shelter shielded the data loggers from direct sunlight (Fig. 3). We calculated mean air temperature during the capture occasions (*TO*) and mean air humidity during the capture occasions (*HO*, measured as difference from the dew point in degrees) from hourly records (days of capture, 10:00 a.m. – 5:00 p.m.). In addition, we calculated mean air temperature (*TI*) and mean hourly precipitation (*PI*) for the intervals between capture occasions.

Capture-mark-recapture analyses

Preparation of the dataset

For site A, we analysed the datasets from all three years together within the same models. For site B, we restricted our analyses to 2020 and 2021, because the very small number of butterflies, ten only, captured in 2019 did not allow for proper fitting of models (Table 1). Also in 2020 and 2021, the number of individuals captured at site B was

Fig. 3. Radiation shelter to protect climate data logger from direct sunlight.

typically low. To ensure reliable model fitting at site B, we decided to pool data from consecutive capture occasions into a single capture event if the time interval between capture occasions was ≤ 3 days and if < 3 individuals were captured at any of the occasions. When the number of butterflies captured on each occasion was equal, we assigned the date in the middle, otherwise all individuals were assigned to the day with more butterflies captured. Pooling data from multiple days of capture violates the assumption of instantaneous sampling and may affect model estimates. Recapture probability can be overestimated and population size on the pooled occasion might be underestimated because the chance of recording a marked butterfly increases when data from multiple days is pooled into one occasion. However, we used restrictive pooling rules, so the bias in the estimates has probably been very small and the total population size estimates were likely unaffected. The capture histories for site A consisted of 15, 18, and 17 occasions in the years 2019, 2020, and 2021. The pooled capture histories for site B consisted of 11 and 13 occasions in 2020 and 2021, respectively, of which six occasions contained pooled data in each year. Analyses of the CMR data were performed in MARK, version 9.0 (White & Burnham 1999), accessed via the RMark 2.2.7 package (Laake 2013) within R statistical software (version 4.1.2, R Core Team 2021).

Estimation of survival and recapture probability

We applied CJS models to examine apparent survival rates (*φ*) and recapture probabilities (*p*) as a function of study year, sex, phenology (represented by the day of the flight season as a linear trend variable, *DOF*), time since marking (*Age*), and wing wear at first capture (*WW*). *WW* approximates butterfly age at first capture whereas *Age* refers to the number of days after first capture. For site A, we were able to fit models with weather variables, in addition to the variables mentioned before. To do so, *TI* and *PI* were used for predicting *φ*, and *TO* and *HO* for predicting *p*. To account for the independence of butterfly generations (i.e. study years), we fixed parameters representing survival between years to zero.

For both sites separately, we first compared 225 different models, including fixed effects of *year, sex*, and *DOF* as well as all possible interactions between the three variables for both, *φ* and *p*. In addition, we tested the fully time specific model, i.e. φ(~ *sex * time*)p(~ *sex * time*), which estimates one parameter for each sampling interval (*φ*) and sampling occasion (*p*). Because many parameters were not estimable in the fully time-specific model, we used φ(~*year * sex * DOF*)p(~*year * sex * DOF*) for goodness-of-fit testing using the bootstrap-ĉ and the median-ĉ approaches implemented in MARK. We adjusted the AICc-values of our models with the highest, i.e. the most conservative, ĉ-estimates. The sum of (quasi-)Akaike model weights is useful for variable selection when all variables have the same number of occurrences within a model set (Burnham & Anderson 2002; Galipaud et al. 2017). To account for

Table 1

Capture events, number of captured individuals and number of individuals that were recaptured at least once. Recaptures on the same day are not considered.

Study site	A						B					
Year	2019		2020		2021		2019		2020		2021	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Capture events	48	14	78	36	75	24	10	3	42	17	60	20
Captured individuals	25	10	33	26	40	18	7	3	24	12	30	17
≥ 1 recaptures	11	3	16	9	21	5	2	0	10	3	11	4

unbalanced variable occurrences within our model sets, we calculated mean model weights (mean w_i, Kittle et al. 2008) across all models with and without a specific predictor variable and we used the ratio between the mean weights (w_i-ratio) as a variable selection criterion. Only predictor variables with a w_i-ratio > 1 (see Supplementary File A, Tables A1, A2) were included into the fixed set of predictors for further modeling.

Second, we added *WW* as an individual covariate and *Age* to the fixed set of predictors for both φ and p. *WW* and *Age* were tested as main effects and in interaction with *sex* but not in interaction with each other, comprising a total of 200 candidate models for site A and 80 candidate models for site B. For site A, we used the same variable selection scheme as described above to update the fixed set of predictors and, third, we added time-specific weather variables to the predictor set: *TO* and *HO* for *p*, *TI* and *PI* for φ. In each model, we tested either effects of temperature (*TO/TI*) or humidity (*HO/PI*) to avoid an overly complex model structure and to account for correlations between the predictors (Pearson correlation *TO*—*HO*: $R = 0.63$, $p < 0.001$). For site B, we could not test for effects of weather variables because of the pooling of capture occasions.

Finally, all models were combined into a final model set, one for each study site. Two candidate models of site A failed to run, the final model set contained 459 different models. For site B, the final set comprised 291 models. After $\hat{c}$-adjustment of the AICc-values, we finally determined the best supported, most parsimonious models from QAICc-values and model weights. We used likelihood-ratio tests to compare between nested models from the same model set. From the best supported model of each site, we estimated mean residence time as $(1 - \varphi)^{-1}$ – 0.5 (Nowicki et al. 2005).

We also tested for weather effects on butterfly recapture probability and apparent survival separately in each year. Goodness-of-fit tests for individual year models were performed with the $\varphi(\sim sex * DOF)p(\sim sex * DOF)$ models. The estimated $\hat{c}$-values gave no indication of overdispersion. Consequently, we determined the best supported models from the AICc-values and model weights without any adjustments.

Estimation of population sizes

We estimated daily population sizes ($\widehat{N}_t$) and total population sizes ($\widehat{N}^*$) from the individual capture histories using the POPAN parameterisation of the JS model (Schwarz & Arnason 1996). In the previous step, CJS models with sex-specific survival and constant recapture probability received strong support at both sites (Tables 2 and 3). We therefore used $\varphi(\sim sex)p(\sim 1)$ as the fixed basis for the POPAN models and we tested models with constant but sex-specific ($\sim sex$), linearly time-dependent ($\sim Time$), quadratic time-dependent ($\sim Time + Time^2$) and fully time-dependent ($\sim time$) probability of entry into the population (*pent*). We also tested for interactive effects of sex and time ($\sim sex * Time$; $\sim sex * (Time + Time^2)$; $\sim sex * time$) on probability of entry. Consequently, our model sets contained seven candidate models for each year and site. We determined the best supported model from each set using AICc-values and model weights. We present estimated daily and total population sizes with their 95 % confidence intervals.

Dispersal analyses

Maximum recorded distances between two capture locations of the

Table 2

Most parsimonious CJS models from a set of 459 candidate models for site A (across all years). We present all models within ΔQAICc < 2 from the best supported model. k denotes the number of parameters in the model.

Name	Model	k	QDeviance	QAICc	ΔQAICc	Weight
A 1	$\varphi(\sim sex)p(\sim 1)$	3	198.709	293.630	0.000	0.029
A 2	$\varphi(\sim sex + WW)p(\sim 1)$	4	285.662	293.811	0.182	0.026
A 3	$\varphi(\sim sex)p(\sim WW)$	4	285.937	294.087	0.457	0.023
A 4	$\varphi(\sim sex)p(\sim DOF)$	4	197.169	294.150	0.521	0.022
A 5	$\varphi(\sim sex * WW)p(\sim 1)$	5	284.116	294.340	0.711	0.020
A 6	$\varphi(\sim sex + DOF)p(\sim 1)$	4	197.622	294.604	0.974	0.018
A 7	$\varphi(\sim sex + WW)p(\sim DOF)$	5	284.550	294.775	1.146	0.016
A 8	$\varphi(\sim sex)p(\sim DOF + Age)$	5	196.137	295.193	1.564	0.013
A 9	$\varphi(\sim sex)p(\sim DOF + WW)$	5	285.005	295.230	1.600	0.013
A 10	$\varphi(\sim WW)p(\sim sex)$	4	287.209	295.359	1.729	0.012
A 11	$\varphi(\sim sex)p(\sim sex)$	4	198.419	295.400	1.770	0.012
A 12	$\varphi(\sim sex)p(\sim HO)$	4	198.422	295.403	1.773	0.012
A 13	$\varphi(\sim sex * WW)p(\sim DOF)$	6	283.097	295.413	1.783	0.012
A 14	$\varphi(\sim sex + WW)p(\sim sex)$	5	285.263	295.488	1.858	0.011
A 15	$\varphi(\sim sex + WW)p(\sim WW)$	5	285.276	295.501	1.871	0.011

same *L. reducta* (LND) were calculated from the coordinates of capture locations in QGIS 3.4.12. Dispersal data of 98 recaptured butterflies (23 females, 75 males) were included in the dispersal analyses.

We used Linear Models (LMs) to test for differences in LND distances between sexes, study sites, and years. We tested whether recorded LND distances depended on the time between the first and last capture of an individual and/or the number of recaptures. Time between first and last capture and number of recaptures were tested as linear and quadratic effects. This was done in separate models due to the high correlation between the variables (Pearson's $R = 0.717$, $p < 0.001$).

Second, we fitted different dispersal kernels to the LND distances of *L. reducta*. In our study, it was not possible to sample the entire study area with equal effort. Instead, sampling was carried out along specific transects. Consequently, the spatial configuration of the transects may have introduced some bias in the frequency distribution of dispersal distances recorded (Robledo-Arnuncio & García 2007), as a previously marked butterfly can only be recaptured on the study transects. We corrected for this bias by calculating an expected frequency distribution of dispersal distances. To do this, we applied a 5 m buffer to the transect routes of each year and created two sets of random points (one each simulating capture and recapture event) along each buffered transect. For each set of random points, the number of points within each buffered transect was proportional to the area of the buffered transect, on average one random point per 100 m^2. Distances between all random points in the first and the second set of points were calculated separately for each study site and year. The distances were grouped into 50 and 100 m bins

Table 3

Most parsimonious CJS models from a set of 291 candidate models for site B (across all years). We present all models within ΔQAICc < 2 from the best supported model. k denotes the number of parameters in the model.

Name	Model	k	QDeviance	QAICc	ΔQAICc	Weight
B 1	$\varphi(\sim sex + WW)p$ (~ 1)	4	147.878	156.196	0.000	0.055
B 2	$\varphi(\sim sex + Age)p$ (~ 1)	4	101.961	156.715	0.519	0.042
B 3	$\varphi(\sim sex + WW)p$ $(\sim Age)$	5	146.764	157.244	1.048	0.032
B 4	$\varphi(\sim sex)p(\sim 1)$	3	104.784	157.409	1.213	0.030
B 5	$\varphi(\sim sex)p$ $(\sim WW)$	4	149.131	157.449	1.253	0.029
B 6	$\varphi(\sim sex + Age)p$ $(\sim WW)$	5	147.258	157.738	1.542	0.025
B 7	$\varphi(\sim Age)p(\sim 1)$	3	105.288	157.913	1.718	0.023
B 8	$\varphi(\sim sex * WW)p$ (~ 1)	5	147.497	157.977	1.781	0.022
B 9	$\varphi(\sim sex * Age)p$ (~ 1)	5	101.076	.157.992	1.796	0.022
B 10	$\varphi(\sim sex)p(\sim Age)$	4	103.249	158.002	1.806	0.022
B 11	$\varphi(\sim sex + WW)p$ $(\sim WW)$	5	147.534	158.014	1.818	0.022
B 12	$\varphi(\sim sex * Age + WW)p(\sim 1)$	6	145.444	158.121	1.925	0.021
B 13	$\varphi(\sim WW)p(\sim sex * DOF)$	6	145.479	158.156	1.960	0.020

and we calculated the frequency of each distance class, corresponding to the expected frequency distribution of dispersal distances. Because the number of recaptured butterflies varied between sites and years, we weighted the expected distributions of dispersal distances by the number of recapture events and finally calculated the relative frequency distribution of expected dispersal distances from the weighted frequencies. We then derived the adjusted frequency distribution of realised LND distances by dividing the observed relative frequency distribution of dispersal distances by the expected relative frequency distribution. Furthermore, we fitted different mathematical models to the adjusted frequency distribution of realised LND distances: (i) the inverse power function (IPF), (ii) the negative exponential function (NEF), (iii) a lognormal mixture model with two components. IPF and NEF were fitted in R statistical software (version 4.1.2, R Core Team 2021) as described in Fric & Konvička (2007). For fitting the lognormal mixture model, we used the R-package mixR 0.2.0 (Yu 2021). We compare the fits visually and do not report statistical metrics because the fitting procedure differs fundamentally between simple and mixed kernels. The mixture distribution is directly fitted to distance class frequencies, whereas the IPF and the NEF are fitted to the inverse cumulative frequencies. In addition, cumulative frequency counts are per sé not independent data points, i.e. reporting R^2- and p-values could pretend false confidence.

To test whether the observed bimodal frequency distribution of LND distances represents behavioural patterns or effects of highly variable time intervals between first capture and last recapture, we fitted the lognormal mixture model twice: (i) to the binned dataset of all 98 LND distances, irrespective of the time interval between the first capture and the last recapture, (ii) to 89 dispersal distances of 62 *L. reducta* individuals that were recorded within a time interval of ≤ 2 d.

Results

Survival and recapture probability

In the single year models run for site A, no overdispersion was detected by any of the goodness-of-fit measures applied ($\hat{c} < 1.036$). Similarly, in the models across years bootstrap goodness-of-fit tests did

not indicate severe overdispersion ($\hat{c} < 1.736$ for both sites). The median-$\hat{c}$ approach indicated some overdispersion for models across years at site A ($\hat{c} = 2.411$) and only slight overdispersion at site B ($\hat{c} = 1.860$). For each site, we used the most conservative estimate of $\hat{c}$ to adjust the AICc-values of our models across years.

The tested models clearly indicated sex-specific apparent survival across the three years at both sites (Tables 2 and 3). On average, models accounting for differences in apparent survival between sexes were 4.3 and 2.1 times more likely for site A and site B, respectively, than models ignoring sex-specific apparent survival (Supplementary File A, Tables A1 and A2). Models with the main effects of *DOF* and *sex* (site A) as well as the interaction of *DOF* and *sex* (site B) as predictors of the recapture probability also received relatively high support (Supplementary File A, Tables A1 and A2). Year had no significant effect on either apparent survival or recapture probability. The time since marking had no effect on the apparent butterfly survival at site A, but we found increasing apparent survival rates with increasing time since marking at site B (likelihood-ratio test model B 2 vs. model B 4: $p < 0.05$). In addition, apparent survival decreased significantly with increasing wing wear of individuals at first capture (Table 2, model A 2; likelihood-ratio test model A 2 vs. A 1: $p < 0.05$; Table 3, models B 1, B 3, B 8, B 11, B 12, B 13; likelihood-ratio test model B 1 vs. B 4: $p < 0.05$; Fig. 4). The tested weather variables had rather weak effects on the apparent survival and recapture probability of *L. reducta* (Table 2; Supplementary Files B and D). Only in 2020, a significant decrease of recapture probability with increasing air temperature and an increase of recapture probability with increasing air humidity were observed. The best supported models across years indicated an apparent daily survival probability of 0.893 for males (95 % confidence interval: 0.864 – 0.916) and 0.753 for females (95 % confidence interval: 0.668 – 0.822) at site A, and of 0.883 for males (95 % confidence interval: 0.833 – 0.919) and 0.665 for females (95 % confidence interval: 0.504 – 0.796) at site B. The apparent survival probabilities translate into mean residence times of eight to nine days for males and two to four days for females. Maximum observed residencies were 31 days for a male (site B) and 11 days for a female (site A). Estimated recapture probabilities were equal among sexes and ranged from 0.307 (95 % confidence interval: 0.250 – 0.371) at site A to 0.354 (95 % confidence interval: 0.255 – 0.466) at site B. At site A, recapture probabilities showed a marginally significant decrease with increasing wing wear or increasing time since the start of the flight season (Table 2, likelihood-ratio tests models A 3 vs. A 1: $p = 0.049$, A 4 vs. A 1: $p = 0.054$).

Population size and phenology

According to the best supported JS models for each year and site (Supplementary File E), estimated total population sizes of *L. reducta* varied between sites and years and ranged from 61 to 123 individuals (Fig. 5). Sex ratios estimated over the entire flight period ranged from 1 : 0.61 to 1 : 1.03 (♂ : ♀). On individual days, abundance of males was significantly higher than that of females.

During the three years of our study, the first individuals were detected on 23 and 24 June at site A. The JS models indicated no protandry with the exception of site A in 2021. Towards the end of the flight season, population sizes of both sexes declined, with the last individuals observed in late July or early August. An exceptionally late observation was made on 15 August 2021, after several survey days without any observation.

Dispersal

Across sites and sexes, average LND distances differed between years ($X^2 = 8.107$, df = 2, $p < 0.05$; Fig. 6). The median of LND distances was below 200 m in 2019 but above 400 m in 2020 and 2021. LND distances increased with an increasing time interval between the first capture and the last recapture of an individual ($X^2 = 22.989$, df = 2, $p < 0.001$) and
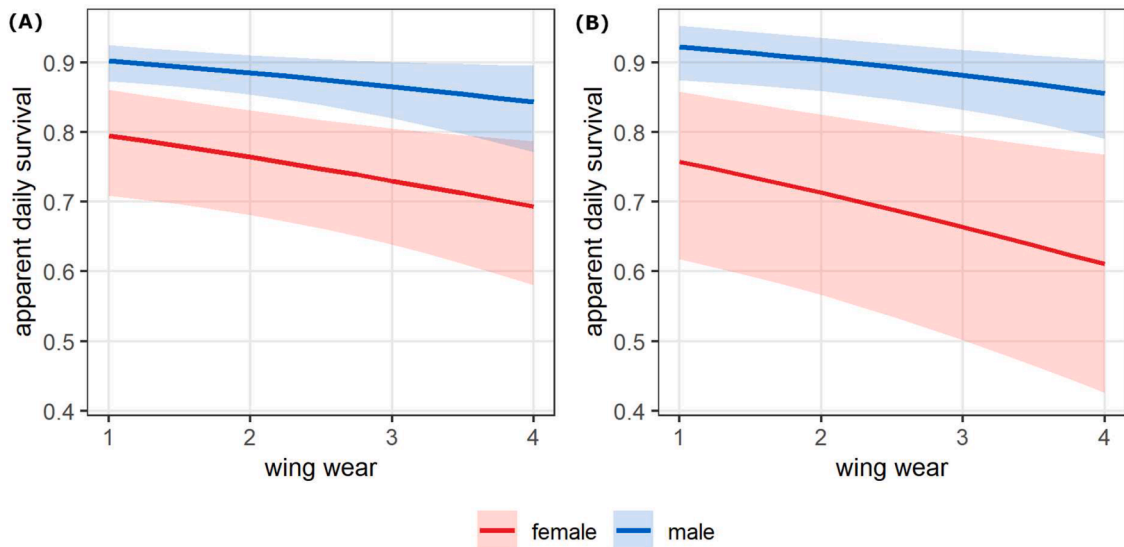
Fig. 4. Effect of wing wear at first capture (*WW, 1 = 'fresh' to 4 = 'heavily worn'*) on the apparent daily survival of individual butterflies in the two study sites. (A) site A, (B) site B. Model predictions according to the best supported models with an effect of wing wear (A 2, B 1).
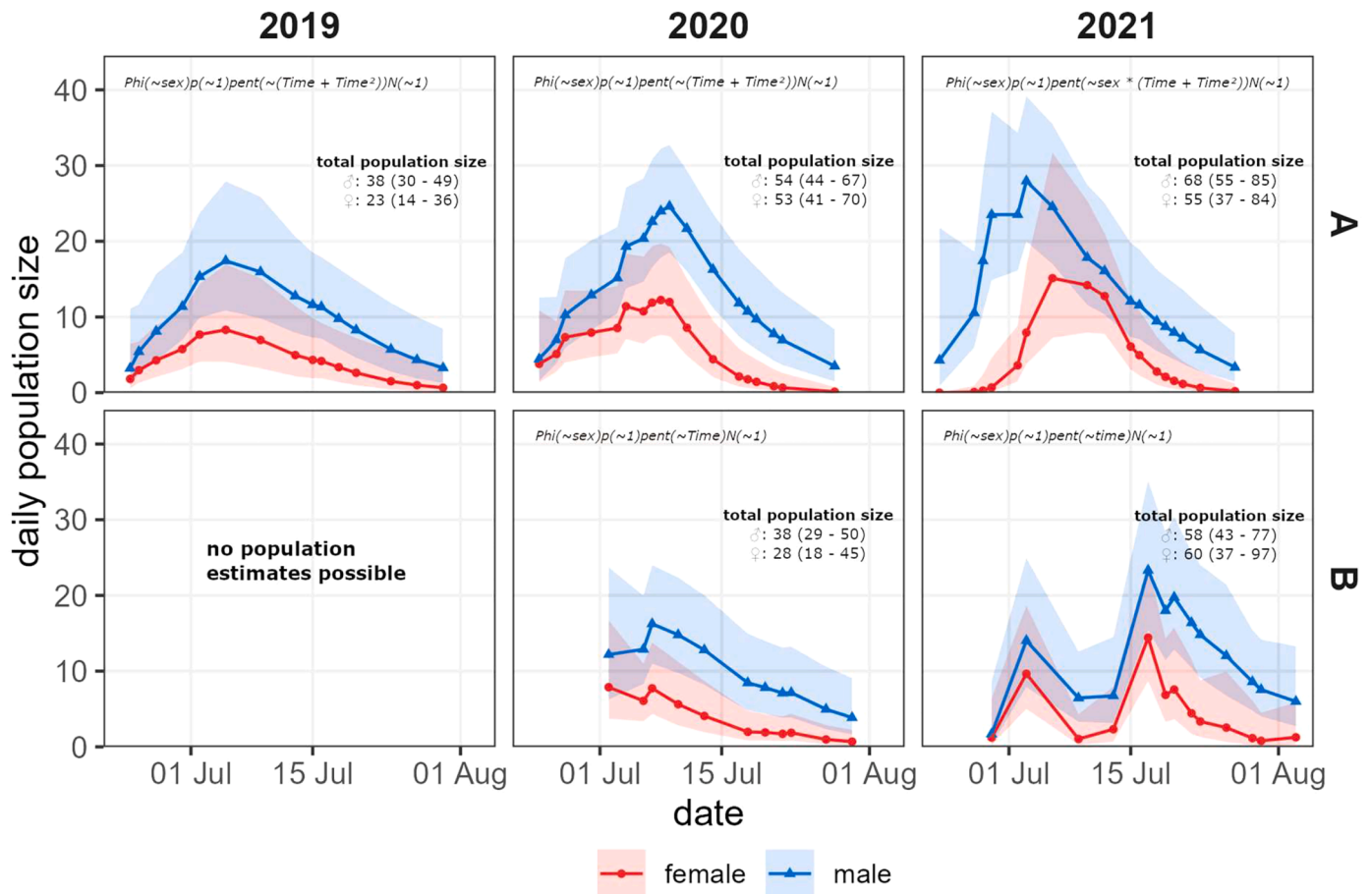

Fig. 5. Year-to-year changes in population sizes of *L. reducta* in two study sites (A, B) in the Swabian Jura (Germany). We present estimated daily population sizes for females (red dots) and males (blue triangles) as well as the estimated total population sizes for both sexes, accompanied by their 95 % confidence intervals displayed in light red and blue. The estimates were generated under the best supported model from a set of seven candidate POPAN models. The best supported model for each dataset is indicated in the top of each panel.

with increasing number of recaptures per individual, at least when relatively few recaptures were made ($X^2 = 8.593$, df = 2, p < 0.01).

Forty-one individual butterflies (42 % of all recaptured individuals)

were captured on at least two different transects, i.e. they must have dispersed through the habitat matrix. Maximum recorded dispersal distances were 1604 m for males and 1135 m for females. We could not
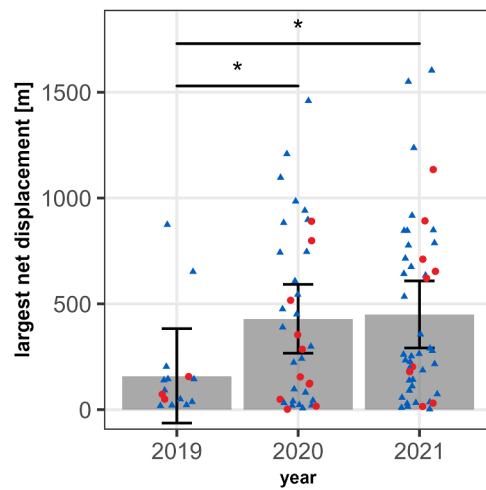
Fig. 6. Largest net displacement distances of *L. reducta* in the three study years. We present predicted median values and 95 % confidence intervals. Red dots and blue triangles represent observed LND distances of females and males, respectively. Mean LND distances did not differ between the sexes. The asterisks indicate significant pairwise differences.

detect longer dispersal distances, although 38 % of all distances covered by our study transects were larger than 1600 m (Fig. 7). The predicted frequencies of long-distance dispersal events differed greatly between the tested dispersal kernels and were highest under the IPF. However, the IPF fitted the observed data poorly. In contrast, the NEF and especially the lognormal mixture model seemed to provide better fits to our data and were consistent in predicting very low probabilities for long-distance dispersal events. The binwidth of the distance classes had no significant effect on the resulting fits (Table 4).

Interestingly, the distribution of LND distances was clearly bimodal and was therefore well fitted by the lognormal mixture model (Fig. 8). LND distances below 300 m and between 600 m and 900 m were observed with higher frequencies than all other distance classes and with higher frequencies than expected due to the transect configuration (Figs. 7 and 8). The bimodal frequency distribution of LND distances was not induced by the highly variable time intervals associated with the individual distances. The influence of the second component of the mixture distribution, and hence the modelled proportion of 'displacement movements' decreased when only distances covered within ≤ 2 days were considered. However, the overall pattern remained the same.
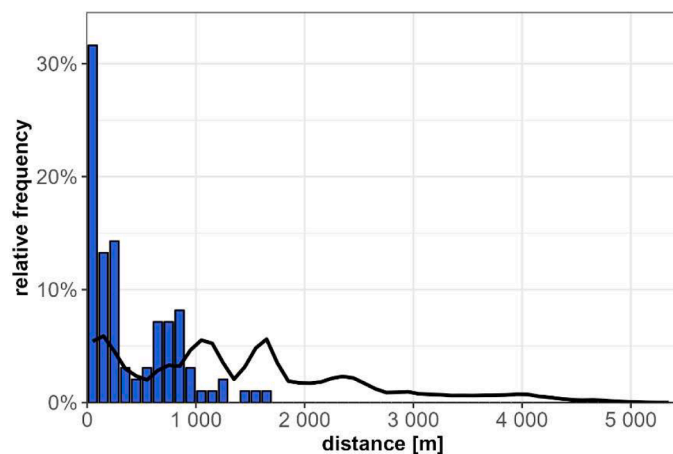
Fig. 7. Observed frequency of largest net displacement distances of 98 *L. reducta* in classes with 100 m binwidth (blue bars) and expected frequency distribution based on the transect configuration (black line).

Discussion

Survival and recapture probability

The apparent survival probabilities of *L. reducta* estimated from our data were similar in both study sites and were constant over the three years of our study. We therefore consider the estimates representative for *L. reducta* populations in Germany, at least for years without extreme weather conditions. The mean life spans derived from the apparent survival rates are in relatively good agreement with the life spans of other European Nymphalidae (Bubová et al. 2016). However, in contrast to most previous results from other butterfly species, we found that apparent survival, and hence mean residency, differs greatly between the sexes of *L. reducta*. One explanation could be that there are true differences in longevity between males and females. Lower survival of females could be explained by their higher attractiveness to predators, resulting from the greater size and the higher absolute fat content compared with males (Ohsaki 1995; Reim et al. 2019). Sex-specific differences in the longevity can also arise due to selective processes. Evolutionary selection may in particular favour the longevity of males as long-lived males can mate multiple times and with different females (Brakefield 1982). However, due to the time limitation of egg-laying in butterflies (e.g. Kőrösi et al. 2008), life span of females should also be under positive selection because long-lived females may reach higher fecundities (e.g. Brakefield 1982; Sielezniew et al. 2020; Wiklund & Persson 1983). Alternatively, the differences in the apparent survival of the sexes could be explained by different dispersal propensities (Ohsaki 1980; Reim et al. 2018). Given that our study populations were open, our estimates of apparent survival are a product of survival and residence. If females emigrated from the study areas more often than males, this could explain their lower apparent survival rates. In several butterfly species elder females tend to emigrate in search for new habitat for their offspring, either as a risk-spreading strategy or to reduce competition, especially if the local density of conspecifics is high (e.g. Kallioniemi et al. 2014; Plazio et al. 2020; Plazio & Nowicki 2021). Unfortunately, our data about the dispersal of females is sparse. At least from this data, we cannot infer any differences in dispersal propensity between the sexes.

Some previous studies have reported age-dependent survival, specifically decreasing survival rates with increasing time since marking (e.g. Brakefield 1982 for *Maniola jurtina*; Osváth-Ferencz et al. 2017 for *Maculinea arion*; Sielezniew et al. 2020 for *Polyommatus daphnis*; Zheng et al. 2007 for *Melitaea cinxia*). In contrast, other studies could not detect age-dependent survival (e.g. Nowicki et al. 2005; Schtickzelle et al. 2002). Recently, Pásztor et al. (2022) demonstrated that body mass and thorax width of *Parnassius mnemosyne* sharply decline with age, which might affect survival and flight capacity of butterflies. We found no correlation between the time since marking and the apparent survival of *L. reducta* at site A, but very unexpectedly, we observed an increase in the apparent survival with increasing time since marking at site B. We hypothesize that the increasing apparent survival with age might be explained by a declining mobility with age, due to either resource depletion, flight muscle decomposition, or setting home ranges (Lebeau et al. 2016; Pásztor et al. 2022). Dispersal propensity might also be higher in the first half of the flight period when butterfly density is high (e.g. Enfjäll & Leimar 2005; Nowicki & Vrabec 2011).

The most supported models for site B indicated that the apparent survival decreased with increasing butterfly wing wear at first capture, and this effect was also significant at site A. This means that butterflies that were older at their first capture and/or have had more fights with predators or conspecifics prior to first capture, had lower apparent survival later. Two reasons are possible: (i) a true decrease of survival with increasing age at first capture / increasing wing damage, (ii) a behavioural polymorphism with more dispersive individuals ('patrollers') having greater wing damage and a higher probability of emigrating from the study area than less dispersive individuals

Table 4

Cumulative proportions of *L. reducta* butterflies moving certain distances. We present unadjusted and adjusted observed frequencies together with model predictions generated under the inverse power function (IPF), the negative exponential function (NEF), and the lognormal mixture model (LogNorm). Predictions were made with binwidths of 50 m and 100 m.

Dist. [m]	Unadjusted frequency [%]	Adjusted frequency [%]	IPF prediction [%]		NEF prediction [%]		LogNorm prediction [%]	
			50 m bins	100 m bins	50 m bins	100 m bins	50 m bins	100 m bins
≥ 200	55.102	66.608	27.060	22.577	78.928	80.655	61.673	61.123
≥ 500	35.714	45.762	14.090	13.486	32.758	33.696	45.418	44.945
≥ 1000	7.143	6.926	8.600	9.132	7.565	7.890	9.421	9.303
≥ 2000	–	–	5.250	6.184	0.403	0.429	0.241	0.074
≥ 5000	–	–	2.733	3.694	0.000	0.000	0.010	0.000
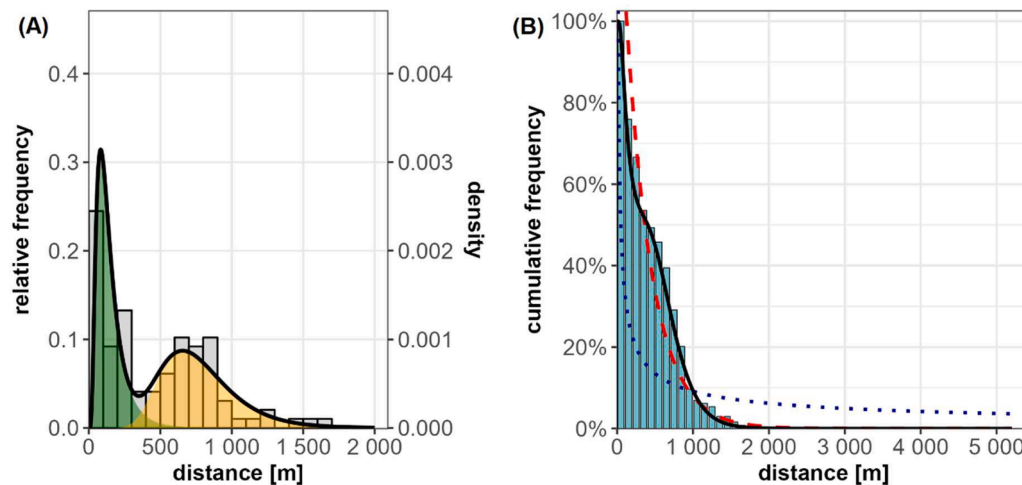
Fig. 8. Distinctive and cumulative proportion of *L. reducta* butterflies moving certain distances. (A) Relative frequency of largest net displacement in 100 m bins, calculated from dispersal data of 98 individual *L. reducta*. Gray bars represent observed data, black lines indicate the probability density predicted under the lognormal mixture model with two components, green and orange areas represent the two components. Frequencies have been adjusted for transect configuration. (B) Reverse cumulative frequency distribution of largest net displacement distances. Blue bars indicate adjusted observed data, lines represent fits of different mathematical models: Blue, dotted: inverse power function (IPF); red, dashed: negative exponential function (NEF); black, solid: lognormal mixture model.

('perchers', cf. Berwaerts et al. 2002). The marginally significant decrease of recapture probability with increasing wing wear at site A could also be explained by this behavioural polymorphism.

Furthermore, some CJS models suggested a decrease of the recapture probability later in the flight season. A general decline in mobility with age and/or time may explain the declining recapture probability, as detectability of flying butterflies is probably much higher than that of resting ones. Male territorial defense flights may have been less frequent at the end of the flight season, when the density of rivals had already decreased. In addition, nectaring sites of *L. reducta* seemed to shift at the end of the flight season from the white-flowered umbellifers on the forest floor to the canopies of lime trees (*Tilia cordata*), where individuals are not available for being captured.

In our models, we tested the effects of temperature and precipitation/humidity on the apparent survival and the recapture probability of *L. reducta* butterflies. While the apparent survival of *L. reducta* was not affected by weather conditions, the recapture probability decreased with increasing air temperature in one out of three years. Vlasanek et al. (2009) investigated the effect of weather conditions on the apparent survival of *Parnassius mnemosyne* but, similar to our study, found no profound correlations. Detecting effects of weather variables on the demography of butterfly populations can be difficult with classical CMR studies for several reasons. As in many other studies on butterflies, we conducted our surveys only on days with favourable weather conditions. The variability in the analysed weather records was therefore relatively low, making it difficult to detect clear correlations between weather variables and the recapture probability. Regarding the effect of weather conditions on adult butterfly survival, two effects may cancel each other out. On bad weather days, butterflies may suffer some weather-related

mortality but are relatively well protected from predator attacks. Conversely, when weather conditions are favourable, butterflies are likely to be more active in flight and therefore more exposed to predation. In addition, rising metabolic rates at high temperatures may cause faster senescence (Niitepõld 2010).

Population sizes and phenology

The JS models indicated rather low population sizes, especially in 2019. Total population sizes of male and female *L. reducta* were relatively equal or only slightly biased towards males. However, daily population sizes differed greatly between the sexes. Only during the peak flight season, the daily abundance of females reached more than ten individuals, whereas male abundances were up to three times higher. The large differences in daily population sizes of male and female *L. reducta* can be explained by the significantly shorter residence time of females (Osváth-Ferencz et al. 2017). Taking into account the approximate size of the study areas, the maximum densities during the peak flight season reached 3.1 and 1.7 individuals per square kilometer for males and females at site A, and 1.2 and 0.7 individuals per square kilometer at site B, respectively. Although local densities at nectaring sites are higher, the numbers indicate that *L. reducta* occurs in very low densities in its last German habitats and underpin the urgent need for conservation measures.

Phenology differed slightly between the two study populations. At site A, the first *L. reducta* were observed on average one week earlier than at site B, probably related to local climatic conditions. The JS models indicated no protandry, except for site A in 2021. While protandry is a typical phenomenon and probably adaptive in many

European butterfly populations (e.g. Kadlec et al. 2010; Osváth-Ferencz et al. 2017; Schtickzelle et al. 2002), negative consequences of protandry could arise under harsh environmental conditions, for example in arctic or alpine environments (Ehl et al. 2019a, 2019b), and in small populations (Calabrese & Fagan 2004). At low local population densities, such as in the case of *L. reducta*, relatively equal emergence of males and females may be advantageous to increase mating opportunities (Bubová et al. 2016).

Except for 2021 at site B, we observed a unimodal trajectory of daily population sizes. Both sexes usually reached peak abundance one to two weeks after the start of the flight period. For some individuals that were about to hatch from the pupa in early July 2021 emergence may have been delayed due to unfavourable weather conditions (rainfall of varying intensity, moderate temperatures), resulting in a shift of peak abundance of about one week. Otherwise, the phenology of *L. reducta* appeared to be relatively stable over the three years of our study. However, one year later, in 2022, the first adults were observed already on 9 June at site A. Consequently, for the first time in the Swabian Jura, a partial second generation was on the wing from early to mid August 2022. The implications of this partial second brood for the populations of *L. reducta* in the Swabian Jura are still unclear and deserve further research. Voltinism of many European butterflies increases in the course of climate warming (Altermatt 2010). In Germany, the occurrence of a (partial) second generation of *L. reducta* is likely to increase in the future.

Dispersal

While male butterflies often return to the same places, for example their defended territories, females typically have straighter flight paths, i.e. they move across the landscape in search of nectar, to avoid male harassment, and to find suitable locations for oviposition (Hovestadt & Nieminen, 2009; Reim et al. 2019; Schultz et al. 2012). Females of *L. reducta* lay their eggs solitarily on the leaves of the host plant. A single female usually lays only one or very few eggs on the same host plant and probably tries to spread the eggs over a larger area to reduce the risk of total reproductive failure due to locally high larval predation, parasitism, or local climatic extreme events (Reim et al. 2019). Longer net displacement distances of females compared with males could therefore be expected. However, our results did not indicate such differences. Nevertheless, we acknowledge that our conclusions about the dispersal of females are limited due to the small number of only 24 individual females that were recaptured. Furthermore, it is possible that we did not detect rare long-distance dispersal flights of single females that might have permanently emigrated from the study area and were therefore not available for recapture.

Only a few CMR studies so far were able to document long-distance dispersal events (e.g. Baguette 2003: 13 km for *Boloria aquilonaris*; Polic et al. 2021: 11.9 km for a male *Argynnis aglaja*), partly due to shortcomings in the study design (Schneider 2003), but also because the chance of recapturing a marked individual strongly decreases with the displacement distance. The maximum recorded displacement distance of *L. reducta* in our study was about 1.6 km, even though it would have been quite possible to record dispersal distances > 1.6 km with the chosen study design (Fig. 7). Movement of adult butterflies between habitat patches carries some risk of mortality. The success of dispersers and the selective advantage of dispersal may depend on the isolation of single habitat patches within a metapopulation (Bergerot et al. 2012; Schtickzelle et al. 2006), the distance between neighbouring metapopulations (Bonelli et al. 2013), the hospitability of the matrix (Nowicki et al. 2014), and the local density of conspecifics (rivals as well as potential mating partners) in the natal and the receiving habitat (Baguette et al. 1998; Hanski et al. 1994; Nowicki & Vrabec 2011).

Interestingly, we observed strong variability in the mean dispersal distance of *L. reducta* between years. On average, dispersal distances were clearly longer in 2020 (mean ± SE: 429 ± 67 m) and 2021 (447 ± 62 m) compared with 2019 (178 ± 64 m). The weather conditions,

which can strongly affect the dispersal of butterflies (Kuussaari et al. 2016), differed only slightly between the years and are therefore an unlikely explanation of the observed year-to-year variability in dispersal distances. However, mean dispersal distances seemed to correlate with population sizes in the respective years, suggesting positively density-dependent dispersal. Increasing dispersal propensity with increasing local density was found in some previous studies (e.g. Enfjäll & Leimar 2005 for *Melitaea cinxia*; Nowicki & Vrabec 2011 for *Maculinea nausithous* and *M. teleius*) whereas others reported negatively density-dependent dispersal (e.g. Baguette et al. 2011 for *Boloria eunomia*; Konvička et al. 2012 for different Melitaeini and Argynnini) or sex-specific effects of density on the emigration propensity, specifically a high emigration rate of males at low female densities and a high emigration rate of females at high male and female densities (Baguette et al. 1998; Plazio et al. 2020).

It has been shown that the IPF, compared to the NEF, can better describe long-distance dispersal of species with a high dispersal power (Baguette 2003) and is more robust for small datasets (Fric & Konvička 2007). However, in the case of *L. reducta*, the NEF provided a much better fit to the data (Fig. 8). Butterfly dispersal studies typically record different behavioural types of movement, e.g. 'routine movement' over relatively short distances and 'displacement movement' over longer distances (Van Dyck & Baguette 2005). This can lead to multimodal dispersal distance kernels. In contrast to the IPF and the NEF, mixture models can explicitly model multiple peaks in the frequency distribution of dispersal data, thus accounting for different types of movement (Hovestadt et al. 2011). In our dataset, the distribution of the LND distances was clearly bimodal. Although we cannot completely exclude the possibility that the bimodal distribution resulted from the specific spatial configuration of the preferred nectaring sites of *L. reducta*, where most individuals were captured, we interpret the pattern as representing different types of movement. Therefore, we strongly believe, that simple dispersal kernels such as the NEF and the IPF cannot properly represent the data-generating processes. The lognormal mixture model fitted the frequencies of LND distances in our study well. Nevertheless, the estimates of long-distance dispersal from the mixed kernel were relatively conservative and of the same magnitude as those from the NEF. With modern computational resources, mixture models offer great potential for realistically describing animal movement (Nathan et al. 2012), and we strongly encourage their use in future butterfly dispersal studies. At the same time, we call for a rigorous evaluation of different mixture models using large capture-mark-recapture datasets or theoretical studies.

Conservation implications and recommendations for habitat management

We observed some variability in the abundance of *L. reducta* between years and the studied habitats, but the population sizes were generally low. Considering that our study areas are among the sites with the highest densities of the species in Germany, the high conservation relevance of *L. reducta* is evident. Forest gaps such as clear-cuts with a size of more than 0.5 ha, and ride edges where the species' host plant grows in sunny conditions provide suitable larval habitat. Improving habitat quality and increasing the area of larval habitat at sites where the species currently occurs will help to increase local population densities and hence dispersal propensity.

Besides improving habitat quality and quantity on a local scale, creating a network of habitat patches on the regional scale is important for the conservation of *L. reducta* and other open forest species that live in SSPs. Our results do not allow any conclusions about the maximum dispersal capacity of *L. reducta*, which could go far beyond the 1.6 km observed in this study. However, our results provide important evidence for conservation planning. About 9 % of the population studied dispersed over more than 1 km. Consequently, we propose to create new habitat patches every 1 to 1.5 km to maximize the chance of successful patch colonization even under relatively low local population densities.

Authors' contributions

HH contributed to the design of the study, led with fieldwork, data analysis, and the writing of the original manuscript. AK supported data analysis and writing of the original manuscript. TG acquired funding, contributed to the design of the study, contributed to fieldwork, and supported writing of the original manuscript. All authors critically revised the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.09.001.

References

Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings Biological Sciences, 277*(1685), 1281–1287. https://doi.org/10.1098/rspb.2009.1910

Baguette, M. (2003). Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography, 26*(2), 153–160. https://doi.org/10.1034/j.1600-0587.2003.03364.x

Baguette, M., Clobert, J., & Schtickzelle, N. (2011). Metapopulation dynamics of the bog fritillary butterfly: Experimental changes in habitat quality induced negative density-dependent dispersal. *Ecography, 34*(1), 170–176. https://doi.org/10.1111/j.1600-0587.2010.06212.x

Baguette, M., Vansteenwegen, C., Convi, I., & Nève, G. (1998). Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*. *Acta Oecologica, 19*(1), 17–24. https://doi.org/10.1016/S1146-609X(98)80004-0

Bergerot, B., Merckx, T., van Dyck, H., & Baguette, M. (2012). Habitat fragmentation impacts mobility in a common and widespread woodland butterfly: Do sexes respond differently? *BMC Ecology, 12*, Article 5. https://doi.org/10.1186/1472-6785-12-5

Bergman, K. O (2001). Population dynamics and the importance of habitat management for conservation of the butterfly *Lopinga achine*. *Journal of Applied Ecology, 38*(6), 1303–1313. https://doi.org/10.1046/j.0021-8901.2001.00672.x

Bergman, K. O., Burman, J., Jonason, D., Larsson, M. C., Ryrholm, N., Westerberg, L., et al. (2020). Clear-cuts are temporary habitats, not matrix, for endangered grassland burnet moths (*Zygaena* spp.). *Journal of Insect Conservation, 24*(2), 269–277. https://doi.org/10.1007/s10841-019-00193-3

Berwaerts, K., Van Dyck, H., & Aerts, P. (2002). Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. *Functional Ecology, 16*(4), 484–491. Retrieved from http://www.jstor.org/stable/826708.

Birch, R. J., Markl, G., & Gottschalk, T. K. (2021). Aestivation as a response to climate change: The great banded grayling *Brintesia circe* in central Europe. *Ecological Entomology, 46*(6), 1342–1352. https://doi.org/10.1111/een.13081

Bonelli, S., Vrabec, V., Witek, M., Barbero, F., Patricelli, D., & Nowicki, P. (2013). Selection on dispersal in isolated butterfly metapopulations. *Population Ecology, 55*(3), 469–478. https://doi.org/10.1007/s10144-013-0377-2

Brakefield, P. M. (1982). Ecological studies on the butterfly *Maniola jurtina* in Britain. II. Population dynamics: The present position. *The Journal of Animal Ecology, 51*(3), 727. https://doi.org/10.2307/4001

Bubová, T., Kulma, M., Vrabec, V., & Nowicki, P. (2016). Adult longevity and its relationship with conservation status in European butterflies. *Journal of Insect Conservation, 20*(6), 1021–1032. https://doi.org/10.1007/s10841-016-9936-0

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.

Calabrese, J. M., & Fagan, W. F. (2004). Lost in time, lonely, and single: Reproductive asynchrony and the Allee effect. *The American Naturalist, 164*(1), 25–37.

Cheeseman, A. E., Cohen, J. B., Whipps, C. M., Kovach, A. I., & Ryan, S. J. (2019). Hierarchical population structure of a rare lagomorph indicates recent fragmentation has disrupted metapopulation function. *Conservation Genetics, 20*(6), 1237–1249. https://doi.org/10.1007/s10592-019-01206-z

Cooper, C. B., & Walters, J. R. (2002). Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology, 16*(2), 471–478. https://doi.org/10.1046/j.1523-1739.2002.00346.x

Cormont, A., Malinowska, A. H., Kostenko, O., Radchuk, V., Hemerik, L., WallisDeVries, M. F., et al. (2011). Effect of local weather on butterfly flight behaviour, movement, and colonization: Significance for dispersal under climate change. *Biodiversity and Conservation, 20*(3), 483–503. https://doi.org/10.1007/s10531-010-9960-4

Ehl, S., Böhm, N., Wörner, M., Rákosy, L., & Schmitt, T. (2019a). Dispersal and adaptation strategies of the high mountain butterfly *Boloria pales* in the Romanian Carpathians. *Frontiers in Zoology, 16*, Article 1. https://doi.org/10.1186/s12983-018-0298-1

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

Enfjäll, K., & Leimar, O. (2005). Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. *Oikos, 108*(3), 465–472. https://doi.org/10.1111/j.0030-1299.2005.13261.x

Franzén, M., Francioli, Y., Askling, J., Kindvall, O., Johansson, V., & Forsman, A. (2022). Differences in phenology, daily timing of activity, and associations of temperature utilization with survival in three threatened butterflies. *Scientific Reports, 12*(1), 7534. https://doi.org/10.1038/s41598-022-10676-0

Franzén, M., Nilsson, S. G., 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., Hula, V., Klimova, M., Zimmermann, K., & Konvička, M. (2010). Dispersal of four fritillary butterflies within identical landscape. *Ecological Research, 25*(3), 543–552. https://doi.org/10.1007/s11284-009-0684-4

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

Galipaud, M., Gillingham, M. A. F., & Dechaume-Moncharmont, F. X (2017). A farewell to the sum of Akaike weights: The benefits of alternative metrics for variable importance estimations in model selection. *Methods in Ecology and Evolution, 8*(12), 1668–1678. https://doi.org/10.1111/2041-210X.12835

German Weather Service (2022). Climate data center. Retrieved from https://cdc.dwd.de/portal/. Accessed September 23, 2022.

Gibbs, M., & van Dyck, H. (2010). Butterfly flight activity affects reproductive performance and longevity relative to landscape structure. *Oecologia, 163*(2), 341–350. https://doi.org/10.1007/s00442-010-1613-5

Griffiths, R. A., & Williams, C. (2000). Modelling population dynamics of great crested newts (*Triturus cristatus*): A population viability analysis. *Herpetological Journal, 10*(4), 157–163.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances, 1*(2), Article e1500052. https://doi.org/10.1126/sciadv.1500052

Hanski, I., Kuussaari, M., & Nieminen, M. (1994). Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology, 75*(3), 747–762. https://doi.org/10.2307/1941732

Hanski, I., & Thomas, C. D. (1994). Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. *Biological Conservation, 68*(2), 167–180. https://doi.org/10.1016/0006-3207(94)90348-4

Harrison, S. (1991). Local extinction in a metapopulation context: An empirical evaluation. *Biological Journal of the Linnean Society, 42*(1–2), 73–88. https://doi.org/10.1111/j.1095-8312.1991.tb00552.x

Hermann, G. (2021). Erkenntnisse aus umfangreichen Daten zur Tagfalter- und Widderchenfauna in zwei Naturräumen. *Artenschutz und Biodiversität, 2*(3), 1–46.

Hesselbarth, G., van Oorschot, H., & Wagener, S. (1995). *Die Tagfalter der Türkei unter Berücksichtigung der angrenzenden Länder*. Harxheim: ConchBooks.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., et al. (2018). Biodiversity along temperate forest succession. *Journal of Applied Ecology, 55*(6), 2756–2766. https://doi.org/10.1111/1365-2664.13238

Hinneberg, H., Döring, J., Hermann, G., Markl, G., Theobald, J., Aust, I., et al. (2022). Multi-surveyor capture-mark-recapture as a powerful tool for butterfly population monitoring in the pre-imaginal stage. *Ecology and Evolution, 12*(8), e9140. https://doi.org/10.1002/ece3.9140

Höttinger, H., Pennerstorfer, J., & Zulka, K. P. (2005). Rote Liste der Tagschmetterlinge Österreichs (Lepidoptera: Papilionoidea & Hesperioidea). *Rote Listen gefährdeter Tiere Österreichs. Checklisten, Gefährdungsanalysen, Handlungsbedarf. Teil 1: Säugetiere, Vögel, Heuschrecken, Wasserkäfer, Netzflügler, Schnabelfliegen, Tagfalter* (pp. 313–354). Grüne Reihe des Bundesministeriums für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Hovestadt, T., Binzenhöfer, B., Nowicki, P., & Settele, J. (2011). Do all inter-patch movements represent dispersal? A mixed kernel study of butterfly mobility in

fragmented landscapes. *The Journal of Animal Ecology, 80*(5), 1070–1077. https://doi.org/10.1111/j.1365-2656.2011.01848.x

Hovestadt, T., & Nieminen, M. J. (2009). Costs and benefits of dispersal in butterflies. *In: J. Settele, T. Shreeve, M. Konvička, & H. Van Dyck (Eds.), Ecology of butterflies in Europe* (pp. 97–106). Cambridge: Cambridge University Press.

Hula, V., Konvička, M., Pavlicko, A., & Fric, Z. (2004). Marsh Fritillary (*Euphydryas aurinia*) in the Czech Republic: Monitoring, metapopulation structure, and conservation of an endangered butterfly. *Entomologica Fennica, 15*(4). https://doi.org/10.33338/ef.84226

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? *Journal of Insect Conservation, 14*(3), 237–246. https://doi.org/10.1007/s10841-009-9250-1

Kadlec, T., Vrba, P., Kepka, P., Schmitt, T., & Konvička, M. (2010). Tracking the decline of the once-common butterfly: Delayed oviposition, demography and population genetics in the hermit *Chazara briseis*. *Animal Conservation, 13*(2), 172–183. https://doi.org/10.1111/j.1469-1795.2009.00318.x

Kallioniemi, E., Zannese, A., Tinker, J. E., & Franco, A. M. (2014). Inter- and intra-specific differences in butterfly behaviour at boundaries. *Insect Conservation and Diversity, 7*(3), 232–240. https://doi.org/10.1111/icad.12046

Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia, 157*(1), 163–175. https://doi.org/10.1007/s00442-008-1051-9

Konvička, M., & Kuras, T. (1999). Population structure, behaviour and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*. in Litovelské Pomoraví, Czech Republic *Journal of Insect Conservation, 3*(3), 211–223. https://doi.org/10.1023/A:1009641618795.

Konvička, M., Novak, J., Benes, J., Fric, Z., Bradley, J., Keil, P., et al. (2008). The last population of the Woodland Brown butterfly (*Lopinga achine*) in the Czech Republic: Habitat use, demography and site management. *Journal of Insect Conservation, 12*(5), 549–560. https://doi.org/10.1007/s10841-007-9087-4

Konvička, M., Zimmermann, K., Klimova, M., Hula, V., & Fric, Z. (2012). Inverse link between density and dispersal distance in butterflies: Field evidence from six co-occurring species. *Population Ecology, 54*(1), 91–101. https://doi.org/10.1007/s10144-011-0277-2

Kőrösi, A., Orvössy, N., Batáry, P., Kövér, S., & Peregovits, L. (2008). Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies. *Oecologia, 156*(2), 455–464. https://doi.org/10.1007/s00442-008-0986-1

Kowalczyk, R., Kamiński, T., & Borowik, T. (2021). Do large herbivores maintain open habitats in temperate forests? *Forest Ecology and Management, 494*, 119310. https://doi.org/10.1016/j.foreco.2021.119310

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., et al. (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters, 13*(5), 597–605. https://doi.org/10.1111/j.1461-0248.2010.01457.x

Kudrna, O. (2002). The distribution atlas of European butterflies. *Oedippus, 20*, 1–342.

Kuussaari, M., Rytteri, S., Heikkinen, R. K., Heliölä, J., & Bagh, P. (2016). Weather explains high annual variation in butterfly dispersal. *Proceedings Biological Sciences, 1835*, 283. https://doi.org/10.1098/rspb.2016.0413

MNHN & OFB (2023). National inventory of natural heritage (INPN). Retrieved from https://inpn.mnhn.fr. Accessed July 20, 2023.

Reinhardt, R., & Bolz, R. (2011). In M. Binot-Hafke, S. Balzer , N. Becker, H. Gruttke, H. Haupt, N. Hofbauer, … M. Strauch (Eds.), Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 3: Wirbellose Tiere: 1 (pp. 167–194). Münster: Landwirtschaftsverlag.

Laake, J. (2013). RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Report 2013-01, 1–25.

Lebeau, J., Wesselingh, R. A., & van Dyck, H. (2016). Floral resource limitation severely reduces butterfly survival, condition and flight activity in simplified agricultural landscapes. *Oecologia, 180*(2), 421–427. https://doi.org/10.1007/s00442-015-3492-2

LepiDiv (2017). Distribution maps of European butterflies and moths. Retrieved from https://www.ufz.de/european-butterflies/index.php?de=43003. Accessed July 20, 2023.

Molleman, F., Javoiš, J., Davis, R. B., Whitaker, M. R. L., Tammaru, T., Prinzing, A., et al. (2020). Quantifying the effects of species traits on predation risk in nature: A comparative study of butterfly wing damage. *The Journal of Animal Ecology, 89*(3), 716–729. https://doi.org/10.1111/1365-2656.13139

Mortelliti, A., Fagiani, S., Battisti, C., Capizzi, D., & Boitani, L. (2010). Independent effects of habitat loss, habitat fragmentation and structural connectivity on forest-dependent birds. *Diversity and Distributions, 16*(6), 941–951. https://doi.org/10.1111/j.1472-4642.2010.00701.x

Mousson, L., Nève, G., & Baguette, M. (1999). Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (lepidoptera, nymphalidae) in Belgium. *Biological Conservation, 87*(3), 285–293. https://doi.org/10.1016/S0006-3207(98)00081-0

Müllerová, J., Szabó, P., & Hédl, R. (2014). The rise and fall of traditional forest management in Southern Moravia: A history of the past 700 Years. *Forest Ecology and Management, 331*, 104–115. https://doi.org/10.1016/j.foreco.2014.07.032

Nathan, R., Klein, E., Robledo-Arnuncio, J. J., & Revilla, E. (2012). Dispersal kernels: Review. *In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), Dispersal ecology and evolution* (pp. 186–210). Oxford University Press. https://doi.org/10.1093/acprof:Oso/9780199608898.003.0015

Niitepõld, K. (2010). Genotype by temperature interactions in the metabolic rate of the Glanville fritillary butterfly. *The Journal of Experimental Biology, 213*(7), 1042–1048. https://doi.org/10.1242/jeb.034132

Nowicki, P. (2017). Survey precision moderates the relationship between population size and stability. *Biological Conservation, 212*, 310–315. https://doi.org/10.1016/j.biocon.2017.06.041

Nowicki, P., Richter, A., Glinka, U., Holzschuh, A., Toelke, U., Henle, K., et al. (2005a). Less input same output: Simplified approach for population size assessment in Lepidoptera. *Population Ecology, 47*(3), 203–212. https://doi.org/10.1007/s10144-005-0223-2

Nowicki, P., & Vrabec, V. (2011). Evidence for positive density-dependent emigration in butterfly metapopulations. *Oecologia, 167*(3), 657–665. https://doi.org/10.1007/s00442-011-2025-x

Nowicki, P., Vrabec, V., Binzenhöfer, B., Feil, J., Zakšek, B., Hovestadt, T., et al. (2014). Butterfly dispersal in inhospitable matrix: Rare, risky, but long-distance. *Landscape Ecology, 29*(3), 401–412. https://doi.org/10.1007/s10980-013-9971-0

Nowicki, P., Witek, M., Skórka, P., Settele, J., & Woyciechowski, M. (2005b). Population ecology of the endangered butterflies *Maculinea teleius* and *M. nausithous* and the implications for conservation. *Population Ecology, 47*(3), 193–202. https://doi.org/10.1007/s10144-005-0222-3

Ohsaki, N. (1980). Comparative population studies of three *Pieris* butterflies, *P. rapae, P. melete* and *P. napi* living in the same area. *Population Ecology, 22*(1), 163–183. https://doi.org/10.1007/BF02513543

Ohsaki, N. (1995). Preferential predation of female butterflies and the evolution of batesian mimicry. *Nature, 378*(6553), 173–175. https://doi.org/10.1038/378173a0

Ojanen, S. P., Nieminen, M., Meyke, E., Pöyry, J., & Hanski, I. (2013). Long-term metapopulation study of the Glanville fritillary butterfly (*Melitaea cinxia*): Survey methods, data management, and long-term population trends. *Ecology and Evolution, 3*(11), 3713–3737. https://doi.org/10.1002/ece3.733

Örvössy, N., Kőrösi, Á., Batáry, P., Vozár, Á., & Peregovits, L. (2013). Potential metapopulation structure and the effects of habitat quality on population size of the endangered False Ringlet butterfly. *Journal of Insect Conservation, 17*(3), 537–547. https://doi.org/10.1007/s10841-012-9538-4

Österling, M. E., Arvidsson, B. L., & Greenberg, L. A. (2010). Habitat degradation and the decline of the threatened mussel *Margaritifera margaritifera*: Influence of turbidity and sedimentation on the mussel and its host. *Journal of Applied Ecology, 47*(4), 759–768. https://doi.org/10.1111/j.1365-2664.2010.01827.x

Osváth-Ferencz, M., Bonelli, S., Nowicki, P., Peregovits, L., Rákosy, L., Sielezniew, M., et al. (2017). Population demography of the endangered large blue butterfly *Maculinea arion* in Europe. *Journal of Insect Conservation, 21*(3), 411–422. https://doi.org/10.1007/s10841-016-9944-0

Ovaskainen, O., & Hanski, I. (2004). From individual behavior to metapopulation dynamics: Unifying the patchy population and classic metapopulation models. *The American Naturalist, 164*(3), 364–377. https://doi.org/10.1086/423151

Pásztor, K., Kőrösi, Á., Gór, Á., Szigeti, V., Vajna, F., & Kis, J. (2022). Phenotypic senescence in a natural insect population. *Ecology and Evolution, 12*(12), e9668. https://doi.org/10.1002/ece3.9668

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

Plazio, E., Margol, T., & Nowicki, P. (2020). Intersexual differences in density-dependent dispersal and their evolutionary drivers. *Journal of Evolutionary Biology, 33*(10), 1495–1506. https://doi.org/10.1111/jeb.13688

Plazio, E., & Nowicki, P. (2021). Inter-sexual and inter-generation differences in dispersal of a bivoltine butterfly. *Scientific Reports, 11*(1), 10950. https://doi.org/10.1038/s41598-021-90572-1

Polic, D., Tamario, C., Franzén, M., Betzholtz, P. E., Yıldırım, Y., & Forsman, A. (2021). Movements and occurrence in two closely related fritillary species. *Ecological Entomology, 46*(2), 428–439. https://doi.org/10.1111/een.12987

R Core Team. (2021). R: A language and environment for statistical computing (Version 4.1.2). *R foundation for statistical computing.*

Reed, D. H. (2004). Extinction risk in fragmented habitats. *Animal Conservation, 7*, 181–191. https://doi.org/10.1017/S1367943004001313

Reim, E., Baguette, M., Günter, F., & Fischer, K. (2018). Emigration propensity and flight performance are decoupled in a butterfly. *Ecosphere, 9*(11), e02502. https://doi.org/10.1002/ecs2.2502

Reim, E., Widderich, F., & Fischer, K. (2019). Sexual differences in the morphology and movement of a butterfly: Good shape does not make good dispersers. *European Journal of Entomology, 116*, 468–476. https://doi.org/10.14411/eje.2019.048

Reinhardt, R., Harpke, A., Caspari, S., Dolek, M., Kühn, E., Musche, M., et al. (2020). *Verbreitungsatlas der Tagfalter und Widderchen Deutschlands.* Stuttgart: Ulmer.

Rhoads, E. A., Williams, P. K., & Krane, C. M. (2017). High inbreeding and low connectivity among *Ambystoma texanum* populations in fragmented Ohio forests. *Ecology and Evolution, 7*(24), 11135–11147. https://doi.org/10.1002/ece3.3637

Robledo-Arnuncio, J. J., & García, C. (2007). Estimation of the seed dispersal kernel from exact identification of source plants. *Molecular Ecology, 16*(23), 5098–5109. https://doi.org/10.1111/j.1365-294X.2007.03427.x

Schneider, C. (2003). The influence of spatial scale on quantifying insect dispersal: An analysis of butterfly data. *Ecological Entomology, 28*(2), 252–256. https://doi.org/10.1046/j.1365-2311.2003.00495.x

Schtickzelle, N., Choutt, J., Goffart, P., Fichefet, V., & Baguette, M. (2005). Metapopulation dynamics and conservation of the marsh fritillary butterfly: Population viability analysis and management options for a critically endangered species in Western Europe. *Biological Conservation, 126*(4), 569–581. https://doi.org/10.1016/j.biocon.2005.06.030

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

Schtickzelle, N., Mennechez, G., & Baguette, M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology, 87*(4), 1057–1065. https://doi.org/10.1890/0012-9658(2006)87[1057:DDWHFI]2.0.CO;2

Schultz, C. B., Franco, A. M. A., & Crone, E. E. (2012). Response of butterflies to structural and resource boundaries. *The Journal of Animal Ecology, 81*(3), 724–734. https://doi.org/10.1111/j.1365-2656.2011.01947.x

Schwarz, C. J., & Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics, 52*(3), 860. https://doi.org/10.2307/2533048

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. *Journal of Insect Conservation, 23*(2), 291–300. https://doi.org/10.1007/s10841-019-00126-0

Sielezniew, M., Kostro-Ambroziak, A., & Kőrösi, Á. (2020). Sexual differences in age-dependent survival and life span of adults in a natural butterfly population. *Scientific Reports, 10*(1), 10394. https://doi.org/10.1038/s41598-020-66922-w

Stefanescu, C., & Jubany, J. (2002). *Limenitis reducta*, una papallona especialista del lligabosc. *Cynthia, 2*, 13–15.

Stevens, V. M., & Baguette, M. (2008). Importance of habitat quality and landscape connectivity for the persistence of endangered natterjack toads. *Conservation Biology, 22*(5), 1194–1204. https://doi.org/10.1111/j.1523-1739.2008.00990.x

Stevens, V. M., Turlure, C., & Baguette, M. (2010). A meta-analysis of dispersal in butterflies. *Biological Reviews of the Cambridge Philosophical Society, 85*(3), 625–642. https://doi.org/10.1111/j.1469-185X.2009.00119.x

Stjernholm, F., Karlsson, B., & Boggs, C. L. (2005). Age-related changes in thoracic mass: Possible reallocation of resources to reproduction in butterflies. *Biological Journal of the Linnean Society, 86*(3), 363–380. https://doi.org/10.1111/j.1095-8312.2005.00542.x

Streitberger, M., Hermann, G., Kraus, W., & Fartmann, T. (2012). Modern forest management and the decline of the Woodland Brown (*Lopinga achine*) in Central Europe. *Forest Ecology and Management, 269*, 239–248. https://doi.org/10.1016/j.foreco.2011.12.028

Šumpich, J., & Liška, J. (2018). New records of butterflies and moths from the Czech Republic, and update the Czech Lepidoptera checklist since 2011. *Journal of the National Museum Prague, Natural History Series, 187*, 47–64. https://doi.org/10.2478/jnmpnhs-2018-0003

Tilman, D., May, R. M., Lehman, C. L., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature, 371*, 65–66. https://doi.org/10.1038/371065a0

Välimäki, P., & Itämies, J. (2003). Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitats - effects of patch characteristics. *Ecography, 26*(5), 679–691. https://doi.org/10.1034/j.1600-0587.2003.03551.x

Van Dyck, H., & Baguette, M. (2005). Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology, 6*(6), 535–545. https://doi.org/10.1016/j.baae.2005.03.005

Vera, F. W. M. (2002). *Grazing ecology and forest history*. Wallingford: CABI.

Vlasanek, P., Hauck, D., & Konvička, M. (2009). Adult sex ratio in the *Parnassius mnemosyne* butterfly: Effects of survival, migration, and weather. *Israel Journal of Ecology and Evolution, 55*(3), 233–252. https://doi.org/10.1560/IJEE.55.3.233

Wahlberg, N., Klemetti, T., Selonen, V., & Hanski, I. (2002). Metapopulation structure and movements in five species of checkerspot butterflies. *Oecologia, 130*(1), 33–43. https://doi.org/10.1007/s004420100775

Warren, M. S., Maes, D., van Swaay, C. A. M., Goffart, P., van Dyck, H., Bourn, N. A. D., et al. (2021). The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences of the United States of America, 118*(2). https://doi.org/10.1073/pnas.2002551117

Wermeille, E., Chittaro, Y., & Gonseth, Y. (2014). *Rote Liste Tagfalter und Widderchen. Gefährdete Arten der Schweiz, Stand 2012*. Bern: Bundesamt für Umwelt / Neuenburg: Schweizer Zentrum für die Kartografie der Fauna.

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

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study, 46*(sup1), 120–139. https://doi.org/10.1080/00063659909477239

Wiklund, C., & Persson, A. (1983). Fecundity, and the relation of egg weight variation to offspring fitness in the Speckled Wood Butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? *Oikos, 40*(1), 53. https://doi.org/10.2307/3544198 (Copenhagen, Denmark).

Yu, Y. (2021). mixR: Finite mixture modeling for raw and binned data (Version 0.2.0). Retrieved from https://CRAN.R-project.org/package=mixR. Accessed January 20, 2023.

Zheng, C., Ovaskainen, O., Saastamoinen, M., & Hanski, I. (2007). Age-dependent survival analyzed with Bayesian models of mark-recapture data. *Ecology, 88*(8), 1970–1976. https://doi.org/10.1890/06-1246.1