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Long-distance movements, large population sizes and density-dependent dispersal in three threatened butterfly species

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Abstract

1. This study investigates the ecology of three threatened butterfly species on a 60 km^2 site in Gotland, Southeast Sweden, using mark–recapture methods from 2017 to 2020.
2. Nearly 30,000 captures were recorded, with average lifespans of 6 days for *Euphydryas aurinia* (Lepidoptera: Nymphalidae) and *Parnassius apollo* (Lepidoptera: Papilionidae) and 2 days for *Phengaris arion* (Lepidoptera: Lycaenidae).
3. Population size, density and maximum flight distances varied between species, with *E. aurinia* at 7.2 km, *P. apollo* at 6.4 km and *P. arion* at 2.5 km.
4. Movement data showed the lognormal kernel fit better than gamma, negative exponential and half-normal kernels for distance travelled per time unit across species and sexes.
5. Generalised linear models revealed significant positive density-dependent emigration and negative density-dependent immigration in all three species.
6. Despite available suitable habitats, these species face threats from limestone quarry expansions, agricultural intensification, modified forestry practices, natural succession and climate change, highlighting the need for proactive conservation and strategic habitat management.

KEYWORDS
butterfly ecology, climate change, density-dependent dispersal, *Euphydryas aurinia* (marsh fritillary), fat-tailed dispersal kernel, Lepidoptera conservation, mark release recapture, metapopulation, *Parnassius apollo* (apollo), *Phengaris (Maculinea) arion* (large blue)

INTRODUCTION

Over the past 50 years, butterflies have become emblematic in studies of ecology, conservation and species responses to environmental perturbations and change (Warren et al., 2021). Typically preferring sun-lit, semi-natural and ephemeral habitats, butterflies seek appropriate areas when existing ones become unsuitable. Consequently, they are susceptible to land-use alterations and climatic shifts, especially in northern Europe's cold and increasingly fragmented environments (Franzen et al., 2022; Kindvall, Franzén, et al., 2022; Sunde et al., 2023).

The primary threat to butterflies emerges from habitat degradation and loss, thus indicating the necessity for targeted management in conserving butterfly species (Warren et al., 2021). The conservation of species associated with semi-natural grasslands presents a formidable challenge, particularly when their survival depends on historically established land-use practices, such as traditional hay mowing, low intense grazing and coppicing. These practices, rooted in historical agricultural methods, are critical for maintaining the habitat conditions necessary for these species. Intense grazing by livestock, such as cattle and sheep, or natural succession following the cessation of grazing also threatens these butterflies (Ellis et al., 2012; Kindvall, Forsman, et al., 2022; Kindvall, Franzén, et al., 2022). Many butterfly species form metapopulations, comprising discrete colonies or patches interconnected by dispersal (Ranius et al., 2011). Although animals are frequently in motion, much of this movement may not be driven by an intrinsic 'desire' to disperse but rather by daily necessities such as foraging and sun basking (Schtickzelle & Baguette, 2003; van Dyck & Baguette, 2005).

Current ecological understanding of butterfly dispersal and its impact on spatiotemporal dynamics predominantly derives from studies focusing on patchy populations in fragmented habitats (Hanski et al., 2011; Hovestadt et al., 2011; Ranius et al., 2011; Shreeve, 1995). These studies have often emphasised isolated populations at increased risk of extinction (Ehrlich & Hanski, 2004; Hill et al., 1996; Nowicki & Vrabec, 2011; Stevens et al., 2010; Thomas, 2005) or species on the edges of their geographical ranges (Hanski, 1998; Thomas et al., 2000). While these insights are invaluable, they may not fully encapsulate the dynamics in environments characterised by extensive, interconnected habitats. Our study fills this gap by providing detailed data on population size and mobility within large, continuous habitats. Such data are important for refining population viability analyses and enhancing management strategies for threatened species in these contexts (Johansson et al., 2017; Meyer, 2000; Thomas & Jones, 1993; van Dyck & Baguette, 2005). Regions with large areas of suitable habitats, harbouring significant populations of species of interest, are often underrepresented in studies of butterflies and warrant more extensive research. This oversight is partly due to challenges in studying vast populations, fluctuating habitat delineations across years and distinguishing routine movements from dispersal (Franzén et al., 2022; Hovestadt et al., 2011). Butterfly research in continuous landscapes, where habitats blur, has been less prioritised because such populations are perceived as less extinction-prone (Baguette & Van Dyck, 2007; Early & Thomas, 2007). To further our understanding of biodiversity patterns and the processes governing them, we must increase our knowledge of the species inhabiting more favourable environments, which requires directing our research attention also towards regions that harbour regionally and locally sustainable populations of endangered species.

Knowledge of density-dependent dispersal and sex-based differences in dispersal strategies is key to better understanding abundance fluctuations and distribution dynamics. Current literature indicates evidence for both positive and negative density dependence impacting emigration and immigration patterns (Enfjäll & Leimar, 2005; Kuussaari et al., 1996; Nowicki & Vrabec, 2011; Schtickzelle & Baguette, 2003). Negative density-dependent dispersal, likely arising from mate scarcity, propels individuals in sparse regions to seek mates (Hanski et al., 1994). High conspecific densities, appealing especially to males, hint at favourable mating conditions and habitable areas (Gilbert & Singer, 1973; King, 1973). Contrastingly, male harassment and competition for resources in high-density populations may drive female dispersal (Enfjäll & Leimar, 2005). Given the nuanced disparities between sexes across taxa, impacting behaviour and population dynamics (Forsman, 1995; Franzén et al., 2022; Legrand et al., 2016), it is imperative to focus on sex-specific differences in dispersal studies (Li & Kokko, 2019).

This study presents a comprehensive analysis of three globally endangered butterfly species—marsh fritillary (*Euphydryas aurinia*, family Nymphalidae), apollo (*Parnassius apollo*, L.) and large blue butterfly (*Phengaris arion* L.), within a landscape with suitable habitats that potentially harbour the world's highest population densities for these species, particularly in years when population sizes are large. This aspect of our study addresses a gap in the existing literature, as unfragmented landscapes have often been overlooked in similar research despite their critical importance for species conservation (Franzen et al., 2022; Franzén et al., 2022; Johansson et al., 2019, 2020; Johansson et al., 2022; Kindvall, Forsman, et al., 2022; Kindvall, Franzén, et al., 2022). The principal objectives of our research were

1. To determine the population size and density of *E. aurinia*, *P. apollo* and *P. arion* within a 60 km^2 landscape on Gotland.
2. To assess and compare the accuracy of four dispersal kernel models—lognormal, gamma, exponential and half-normal—in describing and predicting butterfly movement dynamics.
3. To investigate potential interspecies and sex-based differences in movement and dispersal patterns.
4. To investigate the relationship between density and dispersal and specifically evaluate the hypothesis that there is a positive or negative relationship between local population density (e.g., at the hectare grid level) and the proportion of individuals that depart and arrive in the grids.

To this end, we used an extensive dataset of 29,584 captures, including 16,223 individually marked butterflies (recapture rate of 26%), across 3430-hectare grids (1626 occupied and 1804 unoccupied). This study aimed to enrich our understanding of population numbers and dispersal patterns in populations within natural areas. We underscore the significance of the study area for conserving these threatened butterfly species and posit the necessity for future adaptive management (Serrouya et al., 2019).

MATERIALS AND METHODS

Description of studied species

We focused on three butterfly species: *E. aurinia*, *P. apollo* and *P. arion*. All three species are rapidly declining globally and protected within the European Union (EU), rendering them significant for conservation efforts. They are included in the EU's Habitats Directive

(Council Directive 92/43/EEC) and protected by law within the EU. *Parnassius apollo* is red-listed as near threatened in Europe, *P. arion* as endangered (van Swaay et al., 2010) and *E. aurinia* is in steady decline and is red-listed in many European countries (Eide et al., 2020; Warren et al., 2021). Despite their threatened conservation statuses, they can be locally abundant in certain areas on Gotland (Franzen et al., 2022; Franzén et al., 2022; Johansson et al., 2020) and thus, field studies might allow for robust analyses of population sizes and movements.

Phengaris arion, a blue butterfly, has a wingspan ranging between 32 and 42 mm (Figure S1). It is native to large parts of the western Palaearctic (Europe to China). It is highly localised and thermophilic, associated with dry grasslands. In our study area, it thrives in dry, unfertilised calcareous grasslands and alvar, naturally open due to poor soil and slow humus accumulation (Figure S2). The butterfly is univoltine, active from July to August and visits numerous flowers for nectar. The larvae feed exclusively on *Thymus serpyllum* in our study area. They are adopted by *Myrmica* ants into their nests, where they continue feeding parasitically on ant broods and subsequently hibernate and pupate in June (Tartally et al., 2019; Thomas & Wardlaw, 1992).

Parnassius apollo is a large white butterfly (wingspan ranging from 73 to 87 mm) with variable black and red wing patterns (Figure S1). Its distribution mirrors that of *P. arion*. This iconic butterfly primarily inhabits areas with bare rocks and vegetation-free surfaces. In our study area, it is found on open alvar terrain, naturally kept open due to the lack of vegetation establishment on limestone (Figure S2). Since the 1950s, this butterfly has vanished from large areas, isolating the remaining populations. *Parnassius apollo* is univoltine, with adult activity spanning from June to August. In the study area, adult butterflies predominantly feed nectar from *T. serpyllum* and *Centaurea scabiosa*. The egg overwinters, and larvae exclusively feed on *Sedum album* (Eliasson et al., 2005).

Euphydryas aurinia is an orange-to-brown butterfly with black dots, averaging between 33 and 48 mm in wingspan (Figure S1). Its distribution spans from northern Africa across large parts of Europe to China. Locally, it inhabits rich fens and ungrazed grasslands in our study area (Figure S2) (Franzén et al., 2022; Johansson et al., 2019, 2020; Johansson et al., 2022). *Euphydryas aurinia* is univoltine, active from May to June and feeds exclusively on *Succisa pratensis*. The larvae live gregariously, spin a silk web, bind the food plant leaves together and live and feed within this shelter. After reaching the fourth instar, they hibernate low in vegetation and resume feeding in the spring, with the fully grown larvae pupating in May or June (Eliasson et al., 2005).

Description of the study area

Our study area spans 60 km^2 (10 km $\times$ 6 km) and is located proximal to Slite on the island of Gotland in the Baltic Sea, Sweden (midpoint of the area: 57°69′ N, 18°69′ E) (Figure S3). This region hosts large, continuous populations of butterfly species under investigation (and more), making it one of the last remaining areas in Europe supporting viable populations within a single landscape. A climate with cool summers and cold, rainy winters characterises the area. The average annual temperature is 7.2°C, peaking in July with an average daily temperature of 16.6°C and reaching its lowest in February with an average daily temperature of −2.1°C. The average annual precipitation is 524 mm, with monthly >50 mm from July to January, compared with less than 33 mm from February to June (Persson, 2015). The landscape is remarkably diverse, encompassing 15 habitat types identified by the Habitats Directive (Kindvall, Franzén, et al., 2022). Sections of this area have been subject to extensive livestock grazing, a practice that has intensified since 2000 (Franzen et al., 2022; Franzén et al., 2022; Johansson et al., 2022; Kindvall, Forsman, et al., 2022; Kindvall, Franzén, et al., 2022). Naturally occurring old forests, predominantly pine woodlands, are interspersed throughout the area. The study area is bounded on the west and northeast by agricultural fields where using pesticides, herbicides and inorganic fertilisers is common.

Collection of butterfly occupancy and movement data

The dataset used for this study was collected using a systematic grid approach encompassing the entire study area. A fishnet grid with 100 $\times$ 100 m dimensions (i.e., 1 hectare) was superimposed over the study area, resulting in 3430 hectare grids where butterfly surveys were conducted. In 2017, 1330-hectare grids were surveyed for *E. aurinia*; in 2019, 2359 for *P. apollo* and in 2020, 2256 for *P. arion* (Figure S4). Due to logistical constraints and the limited availability of *P. arion* butterflies in 2018 and 2019, the fieldwork for each species was carried out in different years. Our fieldwork was strategically designed to ensure coverage throughout each butterfly species' lifespan. For *E. aurinia*, we initiated our capture–mark–recapture (CMR) efforts on 26 May 2017 and concluded on 27 June 2017, a span of 33 days, with active CMR implemented on 28 specific days within this period. For *P. apollo*, fieldwork commenced on 14 June 2019 and ended on the 5 August 2019, a span of 52 days, during which CMR was conducted on 47 specific days. Finally, for *P. arion*, our observations began on 10 July 2020 and finished on 4 August 2020, a total span of 26 days, with CMR employed on 23 of those days. Fieldwork was conducted daily between 8 AM and 6 PM on suitable weather days by up to 10 trained field personnel. Surveys were not conducted during unfavourable weather conditions, such as rain (within 1 h after rainfall) and temperatures below 14°C. Each person involved in fieldwork received half a day of training on capturing, identifying, handling, marking and recording data for the captured butterflies. For each butterfly captured, data on species, sex, position and time were recorded.

Fieldwork was organised to maximise coverage of hectare grids, and butterfly observations were recorded along irregular routes to cover all potentially utilised areas within each hectare grid (Figure S2). The Collector app (Esri) was used for data entry in the field. The extensive fieldwork encompassed the entire lifespan and involved regular (daily or bi-daily) inspections of each hectare grid. A strategic rotation of personnel and time was implemented to ensure that all grids were examined at varying times of the day and by different field personnel. In total, 14 persons were engaged in the fieldwork related to *E. aurinia*, 18 for *P. apollo* and 9 for *P. arion*. This study's complexity and rigorous design contribute significantly to the body of research on butterfly populations, aligning with other extensive landscape-scale studies such as those by Schtickzelle et al. (2006) and Nowicki et al. (2014).

Estimating population sizes and lifespan

To estimate population sizes, we divided the study area into northern and southern sectors due to a natural bifurcation created by a large, dense forest (Figure S3). We estimated the population size for each species and geographical sector using the Jolly–Seber method, a technique suited for studying open populations where individuals move between areas (e.g., Seber, 1982). Specifically, we used the Jolly–Seber models implemented in the POPAN module (Arnason & Schwarz, 1999) in Program MARK (White & Burnham, 1999). We opted for a time-dependent recruitment rate more realistic for species with non-overlapping generations (Schtickzelle et al., 2002; Schtickzelle et al., 2003). The selected model, which yielded the lowest Akaike information criterion (AIC) compared with others featuring all possible combinations of constant and varying estimates of the three parameters (capture probability, survival and recruitment), provided daily estimates of local population sizes and seasonal local population size *N* with associated uncertainty. To refine our population density estimates, we divided the Jolly–Seber estimated population sizes across hectare grids based on each grid's highest single-day butterfly counts. The highest single-day butterfly counts in each grid were divided by the estimated total number of butterflies, and this quotient was then multiplied by the maximum number of butterflies marked in 1 day in each grid. This method allowed for a more precise estimation of population density distribution across all hectare grids. The flight period (total number of days of adult occurrence) was used for lifespan estimations. Thus, for example, a flight period from 1 to 10 July corresponds to a lifespan of 10 days.

Calculating the proportion of departures (emigration) and arrivals (immigration) per hectare grid

In examining the per capita movement of butterflies between grid locations, we quantified the departures and arrivals rates to determine the proportion of resident individuals within each grid. Our methodology for calculating these fractions followed the framework established by Hill et al. (1996). Specifically, for a given grid A, the departure fraction (from the entire season) was computed as the number of instances where butterflies marked in grid A were subsequently captured in different grids (emigration), divided by the aggregate number of recapture events for butterflies initially marked in grid A during the entire season (emigration + residents). Conversely, the arrival fraction for grid A was determined by the ratio of recapture events for butterflies marked in other grids but recaptured within grid A (immigration) to the number of resident butterflies in grid A (immigration + residents). This analysis, incorporating population density, species and sex (excluding the species *P. arion* in the analyses of sex differences due to insufficient female individuals captured), aimed to discern the relative influence of local (natality and mortality) versus regional (departures and arrivals) processes on population dynamics, which is pivotal for understanding population structure (Thomas & Harrison, 1992). A predominance of individuals remaining within their initial grids suggests a metapopulation structure composed of discrete local populations. Conversely, significant inter-grid movement implies a more homogenised population dynamic across the landscape (Hanski, 1998; Thomas & Harrison, 1992).

Statistical analyses

Evaluating movement patterns

In this study, we do not distinguish between routine movements and dispersal but consider all movements the same, as inferring the exact moment of departure is challenging, and most long-distance activities represent dispersal events (Jordano, 2017). To study the butterflies' movement patterns, we therefore calculated the distance travelled as the straight-line distance from the last capture point, adjusted for the time elapsed and used dispersal kernel models. Because of the difficulties in measuring dispersal and the need to fit data to rare events such as long-distance dispersal events (Hovestadt et al., 2011; Nathan et al., 2012; Rogers et al., 2019), the best-fitting kernel model still remains a topic of debate (Taleb, 2020), evident in both plant and animal dispersal studies. Because of this, we used and compared four common dispersal kernel models: the half-normal, (negative) exponential, Gamma and lognormal kernels (Nathan et al., 2012).

For dispersal kernel selection, we assessed the performance of the dispersal kernels while incorporating movement data from all three species (with sexes pooled) to identify the kernel that best characterised the general movement patterns. The assessment was conducted using leave-one-out cross-validation, underpinned by Pareto-smoothed importance sampling (PSIS-LOO) (Vehtari et al., 2017). For this, we estimated the posterior distributions of the models using Hamiltonian Monte Carlo as implemented in Stan version 2.31.0 (Team, 2022), interfaced with R through CmdStanR (Gabry & Češnovar, 2020). The posterior distributions were evaluated using the loo package for PSIS-LOO (Vehtari et al., 2022). We used CmdStanR's default settings of four chains for all models, each with 2000 warm-up iterations and 2000 sampling iterations. We relied on the absence of divergent transitions, the R-hat diagnostic and the effective number of samples to assess the reliability of the estimated posterior distributions. The assessment revealed that the dispersal kernel model with the best fit was the lognormal, which was thus used in the subsequent analyses to evaluate potential differences in movement patterns across species and between sexes.

To further assess the performance of the lognormal dispersal kernel, we visually assessed plots of the kernel's complementary cumulative distribution function (CCDF) with the empirical CCDF derived from the recapture data for each species, albeit with sexes pooled together. Following the dispersal kernel selection and evaluation, we modelled the distance travelled as distributed according to a lognormal distribution parameterised by the mean (μ) and standard deviation (σ) of the logged normal distribution. We modelled μ as a linear combination of an intercept (α) and a slope (β) with separate intercepts for each species and separate slopes for each sex. We also used separate standard deviations for each species. Finally, we used standard normal distributions as prior distributions for α and β and negative exponential distributions with rate parameters of 1 as prior distributions for σ. This was done for *E. aurinia* and *P. apollo* separately but not for *P. arion*, which was excluded due to kernel fit problems (Figure 1). We used the lognormal distribution kernel as a foundation to compare the posterior mean distances across the two butterfly species and both sexes. We extracted random samples (10 times per species) from the lognormal distribution to simulate the butterfly's movement over their empirically established average lifespans based on our data.

In our models, where the 'number of days' serves as an input, we defined a function to determine the distribution parameters tailored to each species' specific lifespan. We then aggregated these daily

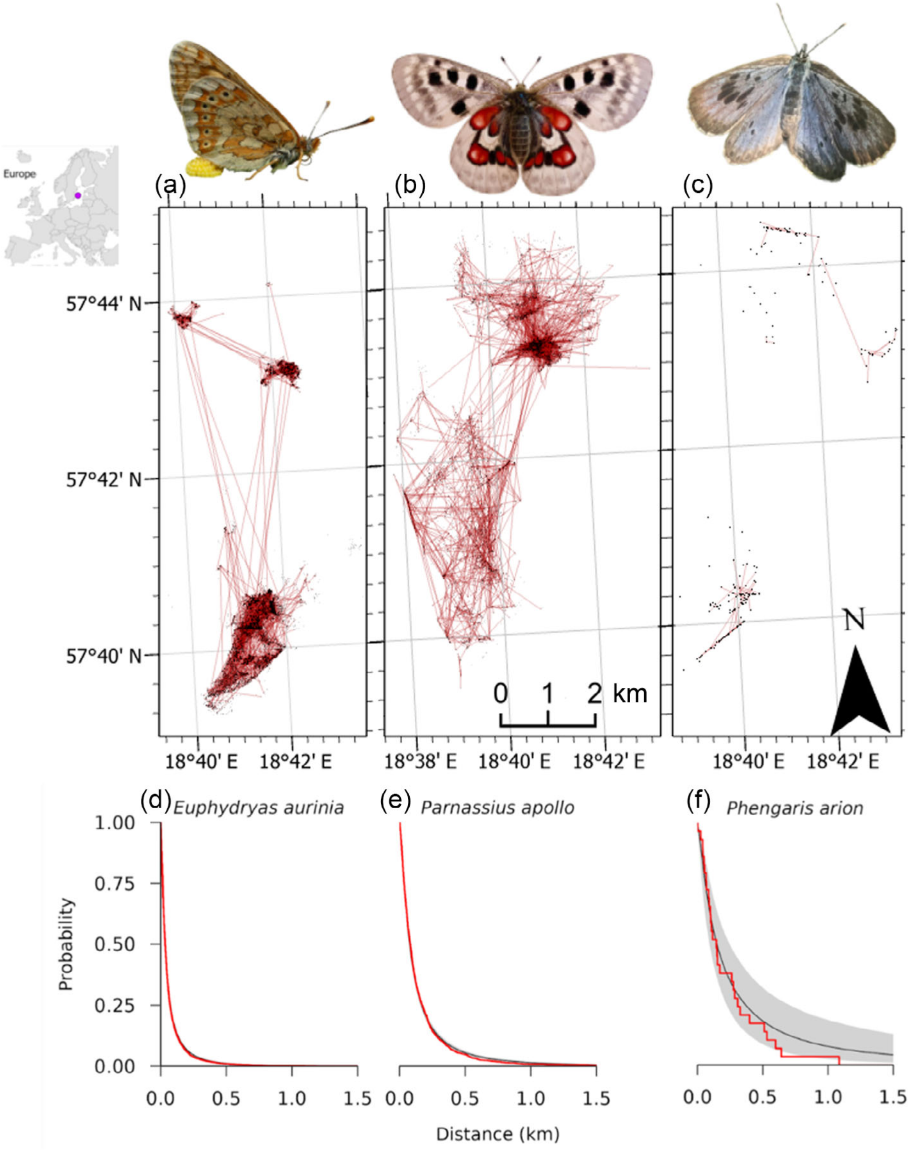

FIGURE 1 Comparative dispersal patterns of three butterfly species: Observations and modelling. Panels (a), (b) and (c) feature the distribution maps of marsh fritillary (*Euphydryas aurinia*), apollo (*Parnassius apollo*) and large blue (*Phengaris arion*), respectively, with each species observed presence represented by dark dots and their movements traced by red lines. Panels (d) through (f) show the modelled likelihood of a butterfly moving a certain distance or greater in a given day based on the complementary cumulative distribution function (CCDF), which is associated with the lognormal movement kernel applied to model butterfly dispersal. At a given distance, '*x*', the CCDF indicates the probability of a butterfly traversing '*x*' or a greater distance within a day. A black line depicts the median, while a shaded region demarcates the 95th percentile interval. The empirical (or observed) CCDF, corresponding to the fraction of observations falling at or below '*x*', is delineated in red. The data for each species were fitted to the kernel separately. Photographs credited to Markus Franzén©.

modelled movements to calculate the total distance a butterfly would cover over its lifespan. Following this, we forecasted the movement trajectories for each of the two species (*E. aurinia* and *P. apollo*) and sex, basing our simulations on the species-specific lifespans and a hypothetical population of 10,000 individuals. This approach enabled us to estimate the proportion of butterflies likely to travel distances exceeding 1, 5 and 10 km within their expected lifespan.

To explore possibly density-dependent migration in the hectare grids, generalised linear models (GLMs) were employed. First, two separate GLMs (one for emigration and one for immigration) were used to assess whether migration was associated with population density or species. For this, the two continuous response variables, emigration (proportion of departures) and immigration (proportion of arrivals) and the two predictor variables, population density in the hectare grid (number of resident butterflies, continuous variable) and species (fixed factor with three levels) were used. Given the presence of overdispersion in the model and the proportion of departing (emigration) and arriving (immigration) per hectare grid as dependent variables, we used a quasi-binomial distribution as the family argument in the GLMs.

To further assess density-dependent effects, we also constructed two separate GLMs for each species (one for emigration and one for immigration) to test for potential sex-specific effects. For this, the same emigration, immigration and population density variables as described above were used, but sex (fixed factor with two levels) and the interaction between population density and sex were also included. This was only done for *E. aurinia* and *P. apollo* because *P. arion* was excluded due to the low number of observations for females. For all of the GLMs, type-III ANOVAs using the Anova function in the car package (version 3.0–2) was used to assess statistical significance of the predictors. Visualisation was accomplished using the ggplot2 and ggeffects packages (Lüdecke, 2018; Wickham & Wickham, 2007), which facilitated the interpretation of the models by offering predicted probabilities for departures and arrivals across different population densities, capture events and species. The R software version 4.3.1 was used for all statistical analyses.

RESULTS

Butterfly occupancy patterns

Euphydryas aurinia occupied 471 of the 1330 surveyed hectare grids in 2017 (35%), *P. apollo* 1141 of the 2359 grids surveyed in 2019 (48%) and *P. arion* 128 of the 2256 surveyed grids in 2020 (6%) (Figures S3–S5). In total, the three butterfly species inhabited 1626 out of the 3430 surveyed grid hectares (Figures S3 and S4). *P. arion* and *E. aurinia* showed no evidence of co-occurrence, whereas *P. apollo* and *E. aurinia* co-occurred in 42 grids and *P. apollo* and *P. arion* in 72 grids (Figure S5). Our results revealed that the average lifespan was 6 days for *E. aurinia* and *P. apollo* and 2 days for *P. arion*.

Population size and density estimates

We marked a total of 16,223 unique butterfly individuals: 10,161 *E. aurinia*, 5902 *P. apollo* and 160 *P. arion*. The butterfly density per visit per grid and recapture rates are detailed in Table 1, revealing significant differences in the average number of individuals marked per visit among the species. Notably, males were recaptured at a higher rate than females for all species, with specific rates and sex ratios provided in Table 1. The estimated population sizes for *E. aurinia* in 2017 were 2415 ± 13 (SE) individuals in the northern area and 17,637 ± 97 in the southern area; for *P. apollo* in 2019, the corresponding numbers were 6554 ± 61 and 6244 ± 79 and for *P. arion* in 2020, 404 ± 60 and 358 ± 53. When distributing the estimated populations in the hectare grids based on the relative butterfly abundances in each grid (proportional maximum number of butterflies marked in 1 day), the mean number of butterflies per occupied grid was 43 (range: 4–334) for *E. aurinia*, 11 (range: 4–160) for *P. apollo* and 3 (range: 3–8) for *P. arion* (Figure S5).

Modelling butterfly movements as the distance travelled per time unit

The maximum flight distance recorded was 7.2 km for *E. aurinia*, 6.4 km for *P. apollo* and 2.5 km for *P. arion* (Figure 1). The observed travel distances per species are presented in Table 2. Evaluating the different dispersal kernels revealed that the lognormal kernel had the highest Expected Log Pointwise Predictive Density (ELPD) when analysing our full dataset (all species and sexes pooled), indicating its superior predictive performance (Table 3). The gamma kernel displayed a ΔELPD (±SE) of −517.9 (± 59.6), which suggests that its ELPD score is 517.9 units inferior to the lognormal kernel. The negative exponential kernel's performance was only marginally worse than the gamma kernel, with a ΔELPD (± SE) of −575.5 (± 67.2), almost

TABLE 1 Summary data from the capture–mark–release data for the three butterfly species studied.

Species	Year	Individuals marked	Density (ind./visit/grid)	♀ Recapture rate	♂ Recapture rate	Sex ratio (♀/♂)
Euphydryas aurinia	2017	10,161	4.42 (0–23.5)	14%	31%	0.35
Parnassius apollo	2019	5902	1.81 (0–7.41)	14%	30%	0.41
Phengaris arion	2020	160	1.12 (0–3)	9%	32%	0.2

Note: It details the number of uniquely marked individuals, the average density of butterflies per grid per visit, and recapture rates with a breakdown by sex, sex ratios and maximum flight distances observed.

TABLE 2 The proportion of individuals in three movement distance classes per species is based on distances between capture events and maximum flight distances observed.

Species	<100 m	100 m–1 km	>1 km	Max. flight distance (km)
Euphydryas aurinia	36%	59%	5%	7.2
Parnassius apollo	15%	63%	22%	6.4
Phengaris arion	13%	71%	16%	2.5

TABLE 3 Comparison of four dispersal kernel models based on all movement data from the three species and the theoretical Expected Log Pointwise Predictive Density (ELPD) for a hypothetical new dataset, as estimated through cross-validation.

Kernel	Probability density function	ΔELPD (±SE)
Lognormal	$f(x;\mu;\sigma) = \frac{1}{x\sigma\sqrt{2\pi}} \exp\left(-\frac{(\ln x-\mu)^2}{2\sigma^2}\right)$	—
Gamma	$f(x;\alpha;\beta) = \frac{\beta^\alpha}{\Gamma(\alpha)} x^{\alpha-1} e^{-\beta x}$	−517.9 (±59.6)
Negative exponential	$f(x;\lambda) = \lambda e^{-\lambda x}$	−575.5 (±67.2)
Half-normal	$f(x;\sigma) = \frac{\sqrt{2}}{\sigma\sqrt{\pi}} \exp\left(-\frac{x^2}{2\sigma^2}\right)$	−8998.8 (±315.4)

Note: The ΔELPD column represents the difference relative to the kernel demonstrating the highest ELPD (specifically, the lognormal kernel), with an accompanying standard error for the component-wise differences. If the ΔELPD value significantly exceeds the standard error, the kernel is expected to exhibit superior predictive performance.

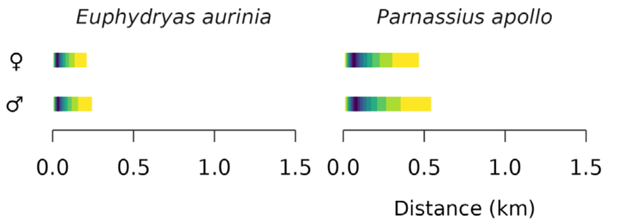

FIGURE 2 Visual representation of butterfly movement as the distance travelled per day: Posterior mean and percentile ranges. The depicted gradient signifies the posterior mean of butterfly movements, transitioning from the 10th percentile interval (illustrated as the darkest shade) to the 90th percentile interval (represented by the lightest shade) in consistent increments of 10.

nine times its standard error, again signalling the superior performance of the lognormal kernel. Finally, the half-normal kernel displayed the least effective performance among the kernels examined, with a ΔELPD (±SE) score of −8998.8 (±315.4), nearly 29 times its standard error. As none of the four dispersal kernels evaluated showed a good fit for *P. arion*, likely owing to the small sample size, this species was excluded from the subsequent modelling based on dispersal kernels.

We reveal differential mobility and dispersal patterns among the butterfly species by integrating empirical observations, modelled likelihoods and simulated projections (Figures 1 and 2 and Table S2). By utilising the posterior mean distances travelled by individuals of both sexes for *E. aurinia* and *P. apollo*, we could delineate distinct mobility profiles for each of the two species and sexes (Figure 2). The simulations of adult lifetime movements provided further insight into the dispersal patterns (Table S2). *Euphydryas aurinia*, the more sedentary species, demonstrated considerably low mobility predictions. Only 11.0% of the males and 9.1% of females were projected to exceed 1 km, and only 0.015% of males and 0.10% of females were predicted to travel 10 km or more (Table S2). In *P. apollo*, 24.7% of the males and 21.8% of females were projected to exceed 1 km, and 0.93% of males and 0.65% of females were predicted to travel 10 km or more (Table S2).

Density-dependent mobility

The GLMs with all data (all species and sexes included) revealed that population density significantly impacted both departure ($\chi^2 = 111.80$, df = 1, $p < 0.001$) and arrival ($\chi^2 = 85.03$, df = 1, $p < 0.001$). Species displayed a significant effect both for departure ($\chi^2 = 50.52$, df = 2, $p < 0.001$) and for arrival ($\chi^2 = 6.28$, df = 2, $p = 0.043$). Our results highlighted that arrival rates decreased and departure rates increased with increasing population density (Figure 3, Table S1). The effect of population density on departure and arrival in a hectare grid was most pronounced in *P. arion*, followed by *P. apollo*, and lastly, *E. aurinia* (Figure 3, Table S1). The analyses of sex-specific emigration and immigration revealed that females significantly arrive and depart less frequently from the grids compared with males and that the effect of population density can differ between the sexes (Table S1; Figure S7). *Parnassius apollo* exhibited a strong density-dependent emigration and immigration and males emigrated to a significantly higher degree when population densities increased compared with females. This observation is substantiated by the interaction term between population density and sex when modelling *P. apollo* emigration (Table S1; Figure S7, $\chi^2 = 6.07$, $p = 0.014$).

DISCUSSION

In our study on three butterfly species (*E. aurinia*, *P. apollo* and *P. arion*) from Gotland, Sweden, we noted high population densities and large distribution areas. We also observed positive density-dependent emigration, negative density-dependent immigration and variations in mobility across species and between sexes within species. Specifically, high local densities were linked to increased departure rates and decreased arrival rates, suggesting that density influences mobility (Nowicki & Vrabec, 2011).

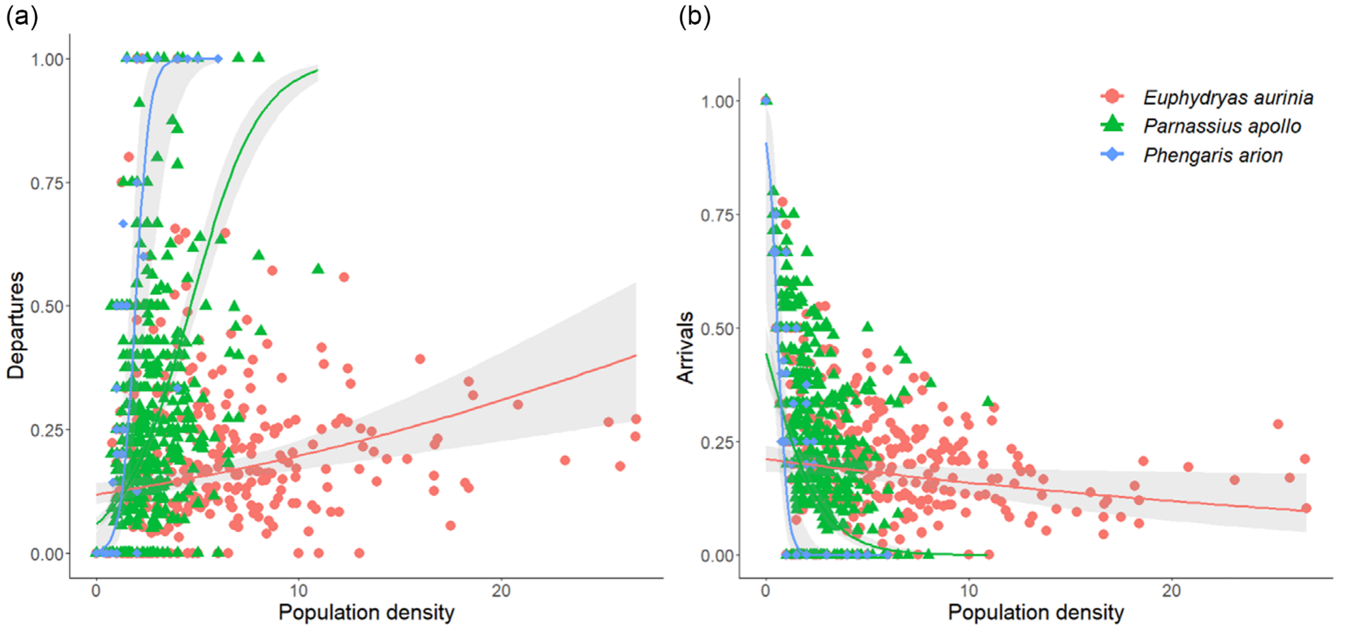

FIGURE 3 Predicted density-dependent probabilities of butterfly movements. (a) Departures: This plot represents the predicted probability of departures across different population densities. (b) Arrivals: Illustrates the predicted probability of butterfly arrivals at different population densities. Colours denote the different species, and grey shaded areas the 95% confidence interval (CI).

Large populations have previously been documented in studies of *P. arion* (Osváth-Ferencz et al., 2017), *P. apollo* (Adamski & Witkowski, 2007) and *E. aurinia* (Zimmermann, Blazkova, et al., 2011), aligning with our findings. For *P. apollo* and *E. aurinia*, we estimated population sizes exceeding 10,000 individuals, with spatial distributions spanning hundreds and, in the case of *P. apollo*, over 1000-hectare grids. Similarly, *P. arion*, despite experiencing a population decline following the 2018 drought, occupied more than 100-hectare grids in our study area. Our research reveals substantial spatial variability in local population densities for these three species, highlighting the complexity of their spatial distribution patterns. Densities in occupied grids varied from 4 to 334 (average 43) for *E. aurinia*, 4 to 160 (average 11) for *P. apollo* and 3 to 8 (average 3) for *P. arion*. These variations, showing potential increases of up to threefold for *P. arion*, 40-fold for *P. apollo* and 80-fold for *E. aurinia*, likely reflect factors such as habitat quality, resource availability and species-specific ecological traits.

Historically, habitats have been dichotomised into suitable or unsuitable, an oversimplification that our findings challenge, advocating for a more nuanced understanding. The intricate spatial and temporal variations in habitats and the mapping of insect densities that can fluctuate substantially across vast expanses present formidable challenges. It thus becomes imperative to identify and judiciously manage core areas, as delineated by Kaszta et al. (2020). These pivotal core areas could serve as essential habitats and donor sites, enriching the broader landscape with essential population dispersals. The imperative of recognising, understanding and characterising these core regions with high population densities cannot be overstated. Such insights guide more effective conservation strategies and pave the way for an evolved conceptual framework in butterfly ecology and, by extension, conservation science.

The recapture data showed that *P. arion* had the shortest flight distances between recaptures (Table 2). This aligns with previous evidence that smaller and more specialised species typically are associated with lower mobility (Stevens et al., 2010). However, despite previous studies labelling *P. arion* as sedentary (Dover & Settele, 2009; Nowicki et al., 2005; Pauler-Fürste et al., 1996; Skórka et al., 2013), our findings indicate significant mobility, with about 16% of *P. arion* individuals having moved over 1 km between capture events (some reaching as much as 2.5 km). This important observation suggests that butterflies assumed to be sedentary and rarely move appear far more mobile than previously understood in landscapes abundant in individuals and extensive, interconnected habitats (Fric, 2010; Hovestadt et al., 2011; Stevens et al., 2010). It should be noted that in 2020, when *P. arion* was surveyed, it was still recovering from the drought repercussions of 2018; thus potentially heightening its mobility that contributed to the re-colonisation of areas from which it had been extirpated. However, given the short lifespan and complex life history of this species, it needs to find the host plant, the prey and a mate within just a few days, which might trigger mobility to find areas where these resources are abundant (Thomas et al., 1989; Thomas & Wardlaw, 1992). In addition, comprehensive studies involving broad geographic ranges and substantial sample sizes have also reported long-distance movements exceeding 10 km in sedentary butterfly species (Polic et al., 2021; Zimmermann, Fric, et al., 2011), and the capacity for long-distance movements in *P. arion* is also supported by recent data from over 1000 marked individuals which highlights potential gene flow across distances up to 90 km (Ugelvig et al., 2012;

personal observation, unpublished). Our Bayesian modelling framework suggests that the distance travelled per day was highest in *P. arion*. However, due to the limited number of observations, ongoing and future studies should confirm this finding.

Our observations showed that the average lifespan were 6 days for *E. aurinia* and *P. apollo* and 2 days for *P. arion*, which is similar to the estimated lifespans reported by Bubová et al. (2016): *P. apollo* 3.73 days (range: 3.20–4.26), *P. arion* 3.53 days (range: 3.07–4.26) and *E. aurinia* 6.40 days (range: 2.24–15.37). When estimating lifetime dispersal distances based on the estimated lifespans and dispersal rates for *E. aurinia* and *P. apollo* (*P. arion* excluded due to insufficient sample size, see Figure S6 and methods for details), the results positioned *E. aurinia* as more sedentary than *P. apollo*, despite it engaging in long-distance movements (Figure 1; Table S2). Both species showed capacity for long-distance dispersal (max flight distance between capture events 7.2 and 6.4 km for *E. aurinia* and *P. apollo*, respectively). However, only 5% of *E. aurinia* travelled >1 km between captures, whereas as much as 22% of *P. apollo* did. The relatively sedentary nature of *E. aurinia*, despite its ability for long-distance movements, suggests that habitat connectivity and local habitat quality are crucial for its survival (Johansson et al., 2019). In contrast, the higher proportion of *P. apollo* individuals undertaking longer dispersals indicates a greater reliance on landscape-level habitat availability, necessitating broader conservation efforts to ensure population persistence.

It should be noted that the three species were each studied in distinct years—2017, 2019 and 2020. Although the years of study were not climatically extreme in contrast to 2018, year-specific weather and temperatures are recognised to influence mobility patterns, often being amplified at higher temperatures (Franzén et al., 2022; Franzén & Nilsson, 2012). Thus, the different mobility capacities we observed across species might be due to habitat preferences, climatic variables and unique life history traits. The assumption that landscapes are homogenous presents another challenge: mobility is matrix and context-dependent (Bonelli et al., 2013). In reality, landscapes exhibit varied features, and a non-homogenous environment could undeniably complicate the findings of a study of this nature (Brown & Kodric-Brown, 1977; Öckinger et al., 2012).

We found positive density-dependent emigration (departures) and negative density-dependent immigration (arrivals) in all three butterfly species. A pattern which is evident in several studies of plants and animals (Rodrigues & Johnstone, 2014) and both positive density-dependent mobility (Nowicki & Vrabec, 2011) and negative density-dependent mobility (Brown & Ehrlich, 1980; Gilbert & Singer, 1973; Ims & Andreassen, 2005; Konvicka et al., 2012; Støen et al., 2006) have been found previously. For example, it is intriguing to note that different studies have identified a negative density-dependent dispersal, hinting at the influence of population densities on dispersal dynamics (Baguette et al., 1996; Baguette et al., 1998; Konvicka et al., 2012; Nowicki & Vrabec, 2011). Interestingly, even contrasting density-dependent mobility has been found for the same butterfly species, the Glanville fritillary *Melitaea cinxia* (Enfjäll & Leimar, 2005; Kuussaari et al., 1996). Our findings indicate that the studied butterfly species tend to emigrate from high-density grids only to immigrate into low-density grids. This is in line with the prevailing belief that animals migrate from high- to low-density regions to minimise resource competition (Solomon, 1949), These movements might be driven by preferences for high-quality habitats (Dunning et al., 1992), predator avoidance (Lima & Dill, 1990) or territorial and individual behaviours (Bowler & Benton, 2005). We found differences in grid fidelity between sexes. Females demonstrated consistent fidelity to grids (Figure S7). This higher site fidelity in females than males align with existing literature suggesting reduced risks and enhanced fitness benefits for females remaining in a consistent area (Bonebrake et al., 2010; Ehl et al., 2018). Future research should focus on detailed analysis of individual butterfly movements and assessments of resource distribution and predation risks.

Beyond contributing to our comprehension of butterfly movement dynamics, our findings highlight the need to evaluate and validate analytical approaches, exemplified by comparing the performance of different dispersal kernel models. In evaluating the dispersal kernels, our findings agree with previous studies that the lognormal kernel may provide a suitable option for modelling and projecting animal and plant movements and dispersal patterns (Bullock et al., 2017; Kindvall, 1999; Nathan et al., 2012). We deem it essential to highlight that the inverse power function (Baguette, 2003; Fric & Konvicka, 2007; Hill et al., 1996; Kuras et al., 2003), although commonly applied in butterfly studies, is excluded from our analysis. Its fundamental flaw lies in its failure to depict a true probability distribution, a perspective echoed by (Nathan et al., 2012). Previous research comparing the utility of various dispersal kernel distribution models has yielded divergent conclusions regarding kernel selection (Bullock et al., 2017; Nathan et al., 2012; Rogers et al., 2019). Despite that no clear consensus has been reached, our results are in line with previous studies which suggest that the lognormal kernel appears most promising for fitting both plant and animal dispersal data (Kindvall, 1999; Nathan et al., 2012; Ovaskainen et al., 2008; Skarpaas et al., 2005). In the future, systematic evaluations of different taxa with varying ecology and sample sizes should be used to strive to reach a consensus about the contexts that may favour the use of specific dispersal kernels.

CONCLUSION AND FUTURE DIRECTIONS

Our findings underscore the need to deepen our knowledge of endangered species' ecology, particularly in areas containing critical populations and habitats. The studied butterfly species symbolise broader European conservation challenges, with their dwindling ranges tied to habitat degradation, human disturbances and climate changes (Warren et al., 2021). It is essential to strategise and manage these critical habitats, primarily as current protected zones may not adequately address the specific needs of these species (Kindvall, Forsman, et al., 2022; Kindvall, Franzén, et al., 2022). Despite the urgency, systematic studies in regions of high population and habitat suitability remain scarce (Thomas, 1995) due to limited resources and focus. Our research reveals that these species inhabit larger areas and move more extensively than previously thought. Future conservation efforts should value and protect these species' distinct nature and habitats. For instance, Gotland offers a unique opportunity to create a biodiversity haven, contrasting the global narrative of habitat loss and biodiversity decline (Newbold et al., 2015; Thomas, 2016). With global biodiversity nearing unsustainable levels, immediate action is needed to ensure long-term sustainability (Newbold et al., 2016).

AUTHOR CONTRIBUTIONS

Markus Franzén: Conceptualization; supervision; project administration; visualization; validation; funding acquisition; writing – original draft; writing – review and editing; investigation; methodology; formal analysis; data curation; resources. **Håkan Johansson:** Formal analysis; visualization; writing – review and editing; writing – original draft. **John Askling:** Project administration; resources; methodology. **Oskar Kindvall:** Conceptualization; methodology; data curation; supervision; resources; project administration; formal analysis; validation; visualization; writing – review and editing; investigation. **Victor Johansson:** Supervision; writing – review and editing. **Anders Forsman:** Methodology; supervision; project administration; writing – review and editing; writing – original draft; investigation; funding acquisition; conceptualization. **Johanna Sunde:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; project administration; data curation; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data associated with this manuscript are not publicly available at this stage due to their sensitive nature, specifically concerning vulnerable species, and their relevance. These data will be disclosed only to the subject matter editor and peer reviewers during the evaluation process. Upon acceptance of this manuscript for publication, all pertinent data will be available from the corresponding author, in accordance with the journal's data-sharing policies.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Generalised linear model results for the impact of population density (number of butterflies/visit) and species on departures and arrivals (per hectare grid). Includes estimates, standard errors (SE), *t*-values and significance levels, denoted as ***for $p < 0.001$, *for $0.01 \le p < 0.05$, (*) for $0.05 \le p < 0.10$ and 'n.s.' for non-significant. Models A and B encompass all three species, whereas C to F are species-separated models (analysing either *E. aurinia* or *P. apollo*), including sex as a predictor.

Table S2. Predicted lifetime movement of butterfly species over distances of 1, 5 and 10 km. This table shows the projected (based on simulations) percentage of individual butterflies expected to exhibit lifetime dispersal distances exceeding 1, 5 and 10 km. The simulations assumed an adult lifespan of 6 days for *E. aurinia* and *P. apollo* and initial population size of 10,000 individuals per sex (male and female) and species.

Figure S1. Photographs of the study species. Featured here are the Marsh Fritillary (*Euphydryas aurinia*) (top left), apollo (*Parnassius apollo*) (top middle) and the apollo caterpillar feeding on the host plant *Sedum album* and the large blue (*Phengaris arion*) (bottom left), each captured post-marking. Photographs: Markus Franzén©.

Figure S2. Habitats on Gotland, southeastern Sweden, associated with select butterfly species. Depicted are habitats for the marsh fritillary (*Euphydryas aurinia*) (top left), apollo (*Parnassius apollo*) (top right) and large blue (*Phengaris arion*) (bottom left). Photographs: Markus Franzén©.

Figure S3. Geographic illustration of the study area and species distribution on Gotland, southeastern Sweden. The map presents the location of the marked individuals from the three studied butterfly species. The distinction by the black diagonal line represents the boundary between the southern and northern study areas utilised in estimating the population sizes of the respective species.

Figure S4. Geographic distribution of surveyed hectare grids for the studied species on Gotland, southeastern Sweden. The maps in this figure illustrate the surveyed grids corresponding to each butterfly species: marsh fritillary (*Euphydryas aurinia*) in the left panel, apollo (*Parnassius apollo*) in the centre panel and large blue (*Phengaris arion*) in the right panel within the study area. Occupied grids for each species are distinctly marked in red, whereas the unoccupied grids are denoted in black.

Figure S5. This figure presents maps illustrating the population densities within each hectare grid for three distinct butterfly species. The left panel depicts the marsh fritillary (*Euphydryas aurinia*), the centre panel shows the apollo (*Parnassius apollo*) and the right panel features the large blue (*Phengaris arion*). Colour gradients represent species-specific density levels, transitioning from blue (indicating low density) to purple (signifying high density). Photographs: Markus Franzén©.

Figure S6. Complementary cumulative distribution functions (CCDF) for four dispersal kernels: Half-Normal, Negative exponential, Gamma and Lognormal. This figure illustrates the CCDF for a given distance '*x*', representing the probability of a butterfly moving '*x*' distance or more within a day. Black lines indicate medians and shaded areas denote the 95th percentile interval. The empirical (or observed) CCDF, which corresponds to the proportion of observations that fall at or below '*x*', is highlighted in red. Each species' data was independently fitted to the respective kernel.

Figure S7. Analysis of departures and arrivals relative to population density, species and sex. This figure presents the outcomes of four separate GLMs exploring the influence of population density and sex on butterfly emigration and immigration rates (see Table S1). The models incorporate interaction terms to examine whether and how these relationships vary between sexes: departure models (top panel) and arrival models (bottom panel).

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