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Distance of movement in three threatened butterfly species

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Abstract

1. Movement is fundamental to population persistence and metapopulation dynamics, but robust comparative estimates of dispersal remain scarce for threatened butterflies. Limited quantitative data on movement constrain effective conservation network design.
2. We focused on three threatened butterfly species—*Euphydryas aurinia*, *Parnassius apollo* and *Phengaris arion*—co-occurring on Gotland, Sweden, which together provide an ideal model for comparative dispersal analysis.
3. To quantify and compare movement patterns among species using extended capture–mark–recapture (CMR) data, test for random-walk behaviour, and identify the best-fitting dispersal kernels.
4. CMR datasets for *E. aurinia* and *P. apollo* were extended to 2024 and combined with comprehensive data for *P. arion*, yielding 9670 net-displacement observations (the distance between the first and last captures) collected from 2017 to 2024. One movement value per individual was used to avoid pseudoreplication, detection probabilities were estimated with Cormack–Jolly–Seber models, and four dispersal kernels were evaluated.
5. Median net displacement differed significantly among species ($\chi^2 = 450.14$, $p < 0.001$): *E. aurinia* showed the lowest value (0.135 km), while *P. apollo* (0.253 km) and *P. arion* (0.252 km) were similar. Movements deviated from random-walk expectations (log–log slope = 0.431 versus 0.5 expected, $p < 0.001$), indicating area-restricted movement. Lognormal kernels best described *E. aurinia* and *P. apollo*, whereas an exponential distribution fitted *P. arion* best, with maximum displacements of 8.19, 10.69 and 4.31 km, respectively.
6. Even butterflies traditionally regarded as sedentary exhibit substantial dispersal capacity. Species-specific movement strategies influence metapopulation connectivity, and the derived parameters provide essential inputs for designing habitat networks within each species's dispersal range.

KEYWORDS
butterfly dispersal, dispersal kernel, endangered species, *Euphydryas aurinia*, *Parnassius apollo*, *Phengaris arion*

INTRODUCTION

Movement is a fundamental component of animal ecology, affecting resource acquisition, mate finding and the distribution and persistence of populations in changing environments (Nathan et al., 2008). For small animals—particularly insects—understanding movement patterns can be crucial for accurate predictions of population dynamics and for guiding effective conservation measures (Hanski, 1998). A key question in movement ecology is whether organisms follow random walk patterns or exhibit more directed movement behaviours, with implications for dispersal distances and population connectivity (Turchin, 1998).

Capture–mark–recapture (CMR) remains one of the primary methods for studying insect movement, despite its inherent limitations. For instance, CMR datasets often contain no precise information about the exact path taken between capture events, requiring researchers to calculate net displacement—the straight-line distance between first and last captures—as a minimum estimate of actual movement. Moreover, differences in detectability among species, populations or individuals can confound comparisons of movement patterns (Lebreton et al., 2003). Nevertheless, CMR analyses provide valuable population-level insights into both demographic parameters and overall spatial ecology in systems where more direct tracking methods are logistically impractical (Franzén et al., 2024b; Nowicki et al., 2014).

Many butterfly species exist in metapopulations, characterised by patches of suitable habitat connected by dispersal events (Hanski, 1998). Understanding these dispersal events—especially how far individuals can move—is key to explaining patch colonisation, persistence in fragmented landscapes, and population viability. Movement patterns can range from area-restricted search within habitat patches to long-distance dispersal between patches, with the relationship between displacement and time revealing whether movements follow random walk expectations or show more complex behaviours (Codling et al., 2008). As movement distance increases, however, the likelihood of recording such events tends to decrease, making it challenging to distinguish routine flights within a patch from longer-range dispersal. Determining the appropriate function (kernel) for describing dispersal distances remains an active area of inquiry in movement ecology, with lognormal, gamma and exponential distributions often used to characterise the right-skewed nature of dispersal data (Logghe et al., 2024; Nathan et al., 2012; Rogers et al., 2019).

In previous publications, we showed that a lognormal dispersal kernel described the movements of *Euphydryas aurinia* and *Parnassius apollo* on Gotland, Sweden (Franzén et al., 2024a; Franzén et al., 2024b). However, that earlier analysis was limited by a shorter time series, the use of sequential movements that violated independence assumptions, and insufficient data for *Phengaris arion*. Here, we extend and refine those findings in four critical ways. First, we incorporate additional years of data for *E. aurinia* and *P. apollo*, thereby improving the statistical power for detecting long-distance movements. Second, we include new, extensive CMR data for *P. arion*, allowing a full interspecific comparison. Third, we explicitly address issues of detectability using Cormack–Jolly–Seber models. Fourth, we use net displacement (one value per individual) rather than sequential movements, ensuring statistical independence, and directly addressing methodological concerns about pseudoreplication.

These enhancements enable us to test four hypotheses: (i) net displacement distances differ significantly among *E. aurinia*, *P. apollo* and *P. arion*, (ii) lognormal dispersal kernels provide the best fit to movement data for all three species, compared with gamma, exponential and half-normal alternatives, (iii) butterfly movements deviate from random walk expectations, showing area-restricted search behaviour, and (iv) despite the inherent limitations of CMR, consistent sampling and detectability analyses allow for meaningful interspecific comparisons.

Taken together, these aims distinguish the present study from our earlier work by incorporating additional years of data, expanding the focal species set, using methodologically robust net displacement calculations, and explicitly evaluating detectability and sampling biases. We argue that *E. aurinia*, *P. apollo* and *P. arion* provide an ideal comparative framework because they are sympatric, share a threatened status and exhibit distinct ecological traits, including host-plant specificity, habitat preferences and potential flight abilities. Hence, each species poses unique challenges for movement estimation, allowing us to test whether common statistical approaches and sampling protocols can reliably capture interspecific differences in mobility. Specifically, we address the following objectives:

1. Interspecific variation: Compare the net displacement patterns of *E. aurinia*, *P. apollo* and *P. arion* using CMR data from 2017 to 2024, under the hypothesis that these butterflies exhibit distinct dispersal capacities based on their ecological requirements and life history traits.
2. Random walk test: Test whether movement patterns follow random walk expectations by examining the relationship between log(displacement) and log(time). Under pure random diffusion, displacement is expected to scale with the square root of time (slope $= 0.5$).
3. Dispersal kernel fit: Evaluate four candidate dispersal kernels (lognormal, gamma, exponential and half-normal) to identify which provides the most appropriate fit for net displacement in each species.
4. Dispersal distances: Estimate the probabilities of reaching particular distances using the best-fitting kernels, highlighting species-specific dispersal capabilities and constraints. We interpret these estimates in light of potential sampling biases, offering recommendations for conservation strategies (e.g. habitat connectivity design) and suggesting complementary approaches (such as genetic analyses) to validate long-distance dispersal events.

MATERIALS AND METHODS

Study species

This study focused on three univoltine butterfly species of high conservation concern in Europe: *Phengaris arion*, *Parnassius apollo* and

Euphydryas aurinia. All three are declining globally, red-listed in multiple European countries and protected under the EU Habitats Directive (Council Directive 92/43/EEC) (Fox et al., 2022; Maes et al., 2019; van Swaay et al., 2010). They co-occur in calcareous and alvar habitats in Gotland, Sweden, providing a robust comparative framework for investigating differences in movement distance.

Phengaris arion is a small lycaenid butterfly (32–42 mm wingspan) with iridescent blue dorsal wings and dark forewing spots. It ranges across the western Palaearctic from Iberia to western China. In the study area, it occupies dry, unfertilised calcareous grasslands and alvar, where sparse vegetation arises from shallow, nutrient-poor soils. Larvae develop exclusively on *Thymus serpyllum* until the fourth instar, after which *Myrmica* ants adopt them; the larvae then overwinter inside the nest and complete development as social parasites (Eliasson et al., 2005; Thomas et al., 1989). Adults are univoltine, emerge synchronously in early July, and typically live only 2–3 days (maximum ∼6 days), necessitating rapid mate location and oviposition (Franzén et al., 2024b). Populations are demographically volatile: annual adult abundance can vary by more than an order of magnitude owing to weather-driven larval survival and stochastic ant–host dynamics (Mouquet et al., 2005; Osváth-Ferencz et al., 2017). These fluctuations, combined with the species' reliance on the spatial co-occurrence of thyme patches and suitable *Myrmica* nests, produce a fine-grained metapopulation structure in which most individuals move tens of metres within a patch. However, rare dispersers recolonise vacant sites kilometres away.

Parnassius apollo is a large white butterfly (73–87 mm wingspan) recognisable by its red and black wing markings. It occurs from Europe to China, but populations have declined markedly since the 1950s. In the study area, *P. apollo* inhabits open alvar landscapes with exposed rock surfaces, where its larvae feed primarily on *Sedum album* (Eliasson et al., 2005; Franzén et al., 2022). Adults are polyphagous nectar feeders and are active from June to August; the species is univoltine (one generation per year). Females lay their eggs individually near host plants, and the fully developed larvae remain inside the eggs over winter, hatching the following spring (Habel et al., 2025). Because *P. apollo* prefers open, warm habitats and has a large wingspan, individuals can fly relatively long distances in search of suitable habitat patches. However, dispersal into suboptimal areas may increase mortality (Brommer & Fred, 1999; Cowley et al., 2001). A recent mark–release–recapture study in the Alps estimated a local population size of ∼480 individuals, with a strongly male-biased sex ratio (∼65% males) (Habel et al., 2025). This suggests that *P. apollo* generally occurs at low densities, which may limit the number of individuals dispersing to colonise new habitats.

Euphydryas aurinia (33–48 mm wingspan) is distinguished by orange-to-brown colouration with black spots. It spans northern Africa, Europe and parts of Asia, but in our region, it is largely restricted to fens and ungrazed grasslands (Eliasson et al., 2005; Franzén et al., 2024b). Larvae feed exclusively on *Succisa pratensis*, while adults visit a variety of nectar sources. A few percent of individuals are capable of dispersing several kilometres to reach new habitat patches (Johansson et al., 2022). The larvae live gregariously in silk webs, which can affect population structure and metapopulation dynamics (Johansson et al., 2019). Although a majority of adults exhibit localised movements around host patches, a smaller fraction may engage in longer dispersal to promote colonisation and gene flow (Warren et al., 1994). Zimmermann et al. (2011) carried out a large-scale mark–recapture study that documented such long-distance movements in *E. aurinia*, demonstrating that even widely separated colonies (on the order of 10–15 km apart) can occasionally exchange individuals. These long-range dispersers, though rare (on the order of only a few individuals out of hundreds), are ecologically significant as they enable recolonisation of empty habitat patches and maintain gene flow among isolated subpopulations. These three species represent distinct ecological profiles, varying in body size, larval host-plant specificity, habitat requirements and degree of specialisation on symbiotic ant nests (*P. arion*), rock outcrops (*P. apollo*), or gregarious larval webs (*E. aurinia*). Such differences enable a comprehensive assessment of how life history traits shape movement and dispersal patterns under comparable sampling conditions in Gotland.

Study area

The research was conducted in a 60 km^2 area (approximately 10 × 6 km) near Slite on the island of Gotland in the Baltic Sea, Sweden (mid-point coordinates: 57°41′ N, 18°41′ E; Fig. S1). This region is notable because it sustains one of the last remaining European landscapes where *P. arion*, *P. apollo* and *E. aurinia* still co-occur in viable populations (Sunde et al., 2024). Habitat diversity is exceptionally high, with at least 15 recognised habitat types under the EU Habitats Directive, making it ideal for examining butterfly movements across varied conditions.

The terrain includes anthropogenically influenced areas (e.g. extensively grazed pastures, some of which have become more intensively managed since 2000) and more natural habitats (e.g. old pine forests on shallow soils). Conventional agricultural fields—using pesticides, herbicides and inorganic fertilisers—border parts of the study area to the west and northeast. The climate is temperate, with a mean annual temperature of 7.2°C. The warmest month is July, averaging 16.6°C, and the coldest is February, at −2.1°C. The average yearly precipitation is 524 mm, with higher monthly rainfall (>50 mm) from July to January compared with the drier period from February to June (<33 mm per month).

Data collection and processing

We standardised sampling effort across habitats and species during their respective flight seasons (Table S1), ensuring consistent survey protocols in terms of routes, times (08:00–18:00 h), and weather conditions (no persistent rain, temperatures ≥17°C). Observers walked slowly in a zigzag pattern, covering all identified suitable habitat for each species and year, provided the weather was suitable (Table S1, Figs. S1***–S3). Adult butterflies were caught using a hand net, marked individually on the underside of the wings with a fine-tipped waterproof marker (Staedtler), and released at the point of capture. The coordinates of each capture were recorded using the Field Maps application (ESRI) with the SWEREF 99 TM projection.

From the CMR data, we calculated net displacement for each butterfly that was captured at least twice. Net displacement was defined as the straight-line Euclidean distance (in kilometres) between the first and last capture locations for that individual. This approach provides one movement value per individual, ensuring statistical independence and avoiding pseudoreplication that would arise from including multiple sequential movements per butterfly. Individuals that were captured only once were excluded from the movement analysis. In total, we analysed net displacement for 9670 individuals (7338 *E. aurinia*, 2041 *P. apollo* and 291 *P. arion*) captured between 2017 and 2024. (*P. apollo* data from 2021 were excluded due to insufficient sample size.)

The size and exact location of the sampled area varied among years, ranging from 1 to 60 km^2 depending on species and logistical constraints (Table S1). While the study design aimed for consistent daily effort, differences in spatial coverage and sampling intensity may have affected the probability of detecting long-distance movements. We addressed potential detectability biases by estimating species-specific detection probabilities using Cormack–Jolly–Seber models, and by focusing on net displacement (which, by definition, filters out intra-patch meandering).

Statistical analysis

All statistical analyses were conducted in R version 4.4.3 (R Core Team, 2024). The packages *glmmTMB* (v1.1.10) (Brooks et al., 2023) for mixed modelling, *multcomp* (v1.4–26) (Hothorn et al., 2016) for post hoc tests, *fitdistrplus* (v1.2–2) (Delignette-Muller & Dutang, 2015) for dispersal kernel fitting, *RMark* (v3.0.0) (Laake, 2013) for capture–recapture analysis, and *emmeans* (v1.10.6) (Lenth, 2022) for estimated marginal means.

Detectability analysis

Detection probability was estimated using Cormack–Jolly–Seber models implemented via RMark (Laake, 2013). We treated each species separately and obtained maximum-likelihood estimates of daily recapture probability (assuming a constant recapture probability over time).

Movement analysis

We calculated net displacement for each individual as described above (one independent movement per butterfly, $n = 9670$). To test whether butterfly movements followed an unbiased random walk, we regressed log(net displacement) against log(time between first and last capture). Under pure random diffusion, the expected slope is 0.5, indicating that mean squared displacement increases linearly with time (Turchin, 1998). We tested whether the observed slope differed significantly from 0.5 using linear regression and a one-sample t-test on the slope estimate. We also examined the relationship between squared displacement and time (i.e., net displacement$^2 \sim$ time interval) for each species using linear regression as an additional assessment of the rate of spatial spread (diffusion rate).

Interspecific comparisons

To test for interspecific differences in net displacement, we fitted a generalised linear mixed model (GLMM) using *glmmTMB*. The response variable was log-transformed net displacement (to improve normality), with species as a fixed effect and year as a random intercept (assuming a Gaussian error distribution). We then performed Tukey's HSD post hoc tests (via *multcomp*) for pairwise comparisons among species whenever the overall species effect was significant. We visualised results using boxplots on a logarithmic scale and used the *multcompView* package to add letter groupings above boxes to indicate statistically distinct groups.

Dispersal kernel fitting

To characterise the dispersal pattern of each species, we fitted four candidate probability distributions—lognormal, gamma, exponential and half-normal—to the observed net displacement data for each species. We used maximum likelihood estimation (fitdist function in *fitdistrplus*) to estimate distribution parameters: μ and σ for the lognormal, α and β for the gamma, λ for the exponential, and σ for the half-normal (mean set to 0 for the half-normal). Model performance was evaluated using Akaike's Information Criterion (AIC). For each species, the distribution with the lowest AIC was selected as the best fit, and we calculated ΔAIC for the alternatives. We also assessed goodness-of-fit visually by comparing empirical displacement histograms to the fitted probability density functions. Once the best-fitting model for each species was identified, we used the model's cumulative distribution function (CDF) to estimate the proportion of individuals expected to exceed specific displacement thresholds (0.1, 0.5, 1, 5, and 10 km). Multiplying these proportions by a hypothetical population of 10,000 individuals provided an intuitive estimate of the number of butterflies (per 10,000) predicted to surpass each distance threshold. This approach highlights both routine and long-distance dispersal probabilities, which can inform metapopulation models and conservation strategies.

RESULTS

A total of 9670 net displacement observations were recorded for the three species from 2017 to 2024 (Table 1). *Euphydryas aurinia*

TABLE 1 Descriptive statistics of butterfly net displacement for the three species (2017–2024).

Species	Individuals (n)	Mean displacement (km)	Median displacement (km)	SD (km)	Mean time (days)	<1 km moves (% of total)	≥1 km moves (% of total)	Max displacement (km)
E. aurinia	7338	0.237	0.135	0.415	6.3	7088 (96.6%)	250 (3.4%)	8.19
P. apollo	2041	0.511	0.253	0.685	6.2	1746 (85.5%)	295 (14.5%)	10.69
P. arion	291	0.456	0.252	0.558	5.1	259 (89.0%)	32 (11.0%)	4.31

Note: Net displacement is the straight-line distance between first and last capture locations for each individual. Mean time between first and last capture is given in days.

TABLE 2 Pairwise species comparisons (Tukey's HSD post hoc tests) for differences in $\log_{10}$(net displacement).

Comparison	β (difference)	SE	z	*p*-value
E. aurinia – *P. apollo*	−0.688	0.038	−18.13	<0.001
E. aurinia – *P. arion*	−0.918	0.078	−11.77	<0.001
P. apollo – *P. arion*	−0.230	0.085	−2.70	0.019

Note: β is the estimated difference in mean $\log_{10}$(km) between species, with standard error (SE), z-value and *p*-value.

exhibited the shortest median net displacement (0.135 km), while *P. apollo* and *P. arion* had similar median displacements (0.253 and 0.252 km, respectively). The maximum recorded displacements were 8.19 km for *E. aurinia*, 10.69 km for *P. apollo* and 4.31 km for *P. arion*. The estimated daily recapture probabilities were: *E. aurinia* $p = 0.223 \pm 0.002$ (SE), *P. apollo* $p = 0.170 \pm 0.004$, and *P. arion* $p = 0.211 \pm 0.014$. The relationship between displacement^2 and time was positive but weak for all species (R^2 ranging from 0.018 to 0.045, $p < 0.01$ in each case). *P. apollo* showed the steepest increase in area covered over time (slope ≈ 0.110 km^2/day), indicating the fastest spatial spread, whereas *E. aurinia* spread the slowest (slope ≈ 0.028 km^2/day).

Net displacement varied significantly among species (likelihood-ratio $\chi^2 = 450.14$, df $= 2$, $p < 0.001$; Table 2). Overall, *E. aurinia* moved the least, and *P. apollo* the most, with *P. arion* intermediate. Short-distance movements (<1 km) accounted for 96.6% of *E. aurinia*'s displacements, 85.5% of *P. apollo*'s, and 89.0% of *P. arion*'s (Table 1). Pairwise comparisons of log-transformed displacements indicated that *E. aurinia* travelled significantly shorter distances than both *P. apollo* and *P. arion* (Tukey HSD, both $p < 0.001$). While *P. apollo* and *P. arion* had similar median displacements (Table 1), *P. arion* showed a slightly but significantly greater mean displacement on the log scale compared with *P. apollo* (Table 2). Figure 1 illustrates the distribution of net displacements by species on a $\log_{10}$ scale, with *E. aurinia* having a much more constrained range relative to the other two species.

When examining the temporal scaling of movement, the log–log regression of displacement versus time revealed a slope of 0.431 (± 0.015 SE) for all species combined, which is significantly lower than the 0.5 expected under an unbiased random walk (F_1,9668 $= 21.92$, $p < 0.001$). Thus, on average, butterfly displacement increased more slowly than the square root of time, deviating from simple diffusion.

Fitting dispersal kernels to the net displacement data showed that the lognormal distribution provided the best fit for *E. aurinia* and *P. apollo*, whereas an exponential distribution best fit the *P. arion* data (Figure 2; Table S2). For *E. aurinia*, the lognormal had mean (μ) $= -2.13$ and SD (σ) $= 1.27$ on the natural log scale, while for *P. apollo* $\mu = -1.38$ and $\sigma = 1.11$. In contrast, *P. arion*'s displacements were best captured by an exponential distribution with rate parameter $\lambda = 2.28$ km^{-1} (implying a mean displacement of ~0.44 km). Model comparisons showed substantial differences: for *E. aurinia* and *P. apollo*, the lognormal outperformed gamma, exponential, and half-normal alternatives by ΔAIC >10 in all cases. For *P. arion*, the exponential was markedly better than the lognormal (ΔAIC ≈ 18.5), with gamma and half-normal trailing far behind (ΔAIC >15,000; see Table S2). The heavy right tail of the lognormal effectively captured the rare long-distance movements of *E. aurinia* and *P. apollo*, whereas *P. arion*'s movement distribution decayed much more sharply.

Using the best-fit kernels, we estimated the proportions of individuals expected to exceed various distances (Table 3). For instance, the model predicts that about 55.1% of *E. aurinia* individuals move at least 0.1 km (100 m) during their observed lifespan, compared with 76.4% of *P. apollo* and 80.3% of *P. arion*. At the 1 km threshold, ~14.2% of *P. apollo* are expected to disperse ≥1 km, versus ~11.1% of *P. arion* and ~4.1% of *E. aurinia*. The right-tail differences are especially pronounced: an estimated 1.01% of *P. apollo* individuals travel ≥5 km (approximately 101 out of 10,000), compared with just 0.11% of *E. aurinia* (~11 per 10,000) and essentially 0% of *P. arion*. Indeed, the extrapolated number of *P. arion* expected to exceed 5 km in a sample of 10,000 was effectively zero, reflecting the steep drop-off of its exponential dispersal curve. These quantitative predictions underscore that while most individuals of each species move relatively short distances, *P. apollo* produces long-distance dispersers at a substantially higher rate than the other two butterflies.

DISCUSSION

Our results reveal distinct movement patterns among the three studied butterfly species. Based on net displacement analysis, the species showed broadly similar median movements (~0.13–0.25 km), but differed significantly in their overall movement distributions ($\chi^2 = 450.14$, $p < 0.001$). Notably, all three species showed a greater capacity for movement than some earlier field studies suggested. *Parnassius apollo* exhibited the maximum recorded displacement of 10.69 km, followed by *E. aurinia* at 8.19 km and *P. arion* at 4.31 km. The most striking finding is that despite similar median displacements,

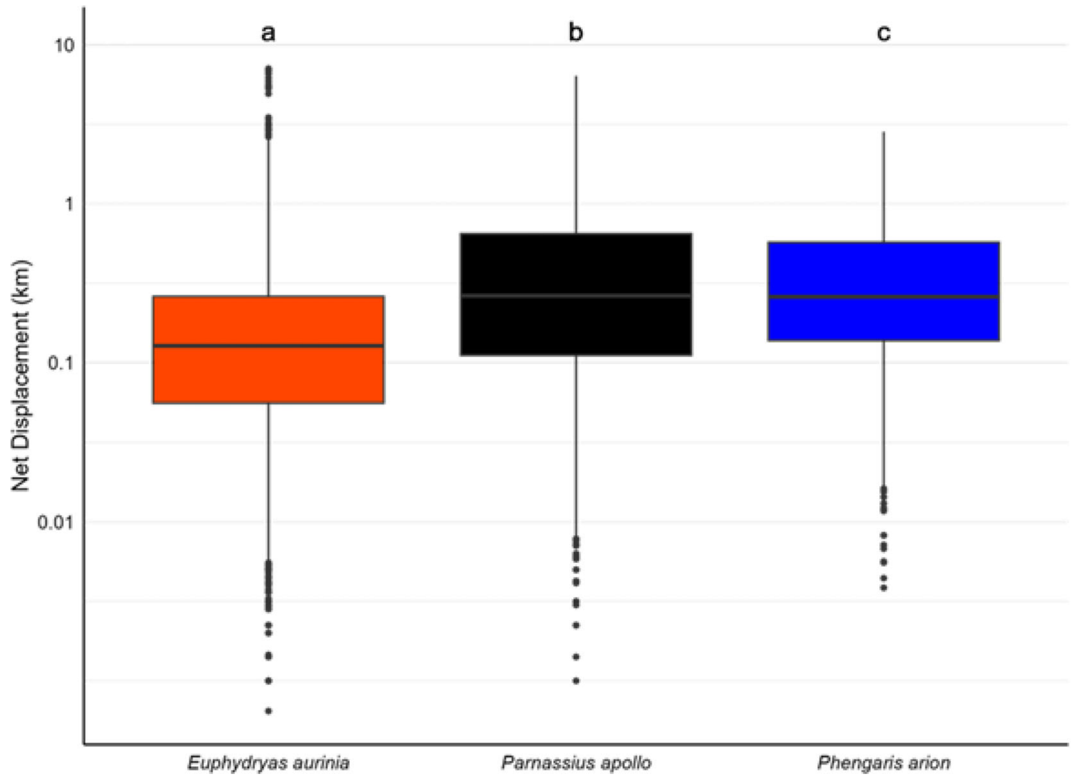

FIGURE 1 Boxplots of net displacement for three butterfly species (*Euphydryas aurinia*, *Parnassius apollo* and *Phengaris arion*) on a $\log_{10}$ scale. Boxes span the interquartile range (IQR) with the median indicated by a horizontal line. Whiskers extend to the smallest and largest values within 1.5 × IQR; points beyond are shown as individual dots (outliers). Different letters above boxes indicate groups that differ significantly ($p < 0.05$) based on Tukey's HSD post hoc comparisons. Net displacement represents the straight-line distance between first and last capture locations for each butterfly (one displacement per individual).

the species differed markedly in their propensity for long versus short moves: about 14.5% of *P. apollo* individuals moved ≥1 km (Table 1), roughly four times the proportion in *E. aurinia* (3.4%). In other words, *P. apollo* undertook long flights much more frequently than *E. aurinia*, with *P. arion* intermediate (11.0% ≥1 km). This result for *P. arion* is especially notable because it challenges the prevailing view that *P. arion* and related *Phengaris* (formerly *Maculinea*) species are largely sedentary (Dover & Settele, 2009; Nowicki et al., 2005; Pauler-Fürste et al., 1996; Simcox et al., 2024). Instead, our data show *P. arion* frequently moving hundreds of metres and occasionally over a kilometre, aligning with genetic evidence for gene flow over distances up to ~90 km in this species (Ugelvig et al., 2012). The observed mobility of *P. arion* is plausibly linked to its complex life history, which necessitates finding suitable *Thymus* host plants in proximity to *Myrmica* ant nests, though females likely assess ant presence indirectly through plant chemical cues such as monoterpenoid volatiles rather than detecting ants directly (Patricelli et al., 2015; Thomas et al., 1989; Thomas & Wardlaw, 1992). Moreover, the relatively continuous calcareous grassland landscape in Gotland may facilitate movement; in contrast, *P. alcon* in a more fragmented region shows very restricted movement and strong genetic structuring (Vanden Broeck et al., 2017). Our expanded dataset and focus on net displacement thus reveal that even butterflies often considered "sedentary" can display appreciable dispersal ability under favourable landscape conditions.

We found that the displacement–time scaling of movement deviates significantly from a simple random walk. The subdiffusive scaling exponent (~0.43) derived from the log–log regression is below the 0.5 expected for unbiased diffusion, indicating area-restricted search behaviour. This aligns with Kőrösi et al. (2008), who found that *Maculinea rebeli* females established home ranges rather than dispersing widely, with time constraints on egg laying increasing the costs of movement. In practical terms, this means that these butterflies tend to slow down and remain within a limited area when in resource-rich or suitable habitat, rather than wandering randomly over larger distances. Similar patterns have been observed in other insects: individuals take shorter steps and make more frequent turns in high-quality habitat patches, concentrating their search where resources are abundant (i.e., exhibiting area-restricted search behaviour) (Bussan & Schultz, 2023; Kindvall, 1999). By contrast, when resources are scarce or butterflies venture outside their habitat patches, they tend to fly in straighter paths with longer step lengths, yielding movement patterns closer to random diffusion (Fownes & Roland, 2002; Ross et al., 2005). Such context-dependent movement strategies – intensive local search versus directed long-range movement – suggest that all three species spend the majority of their time foraging and searching within habitat patches (thus limiting their overall diffusion rate), but are still capable of relatively straight, long flights during inter-patch dispersal. This behaviour reflects a trade-off between efficiently exploiting local resources

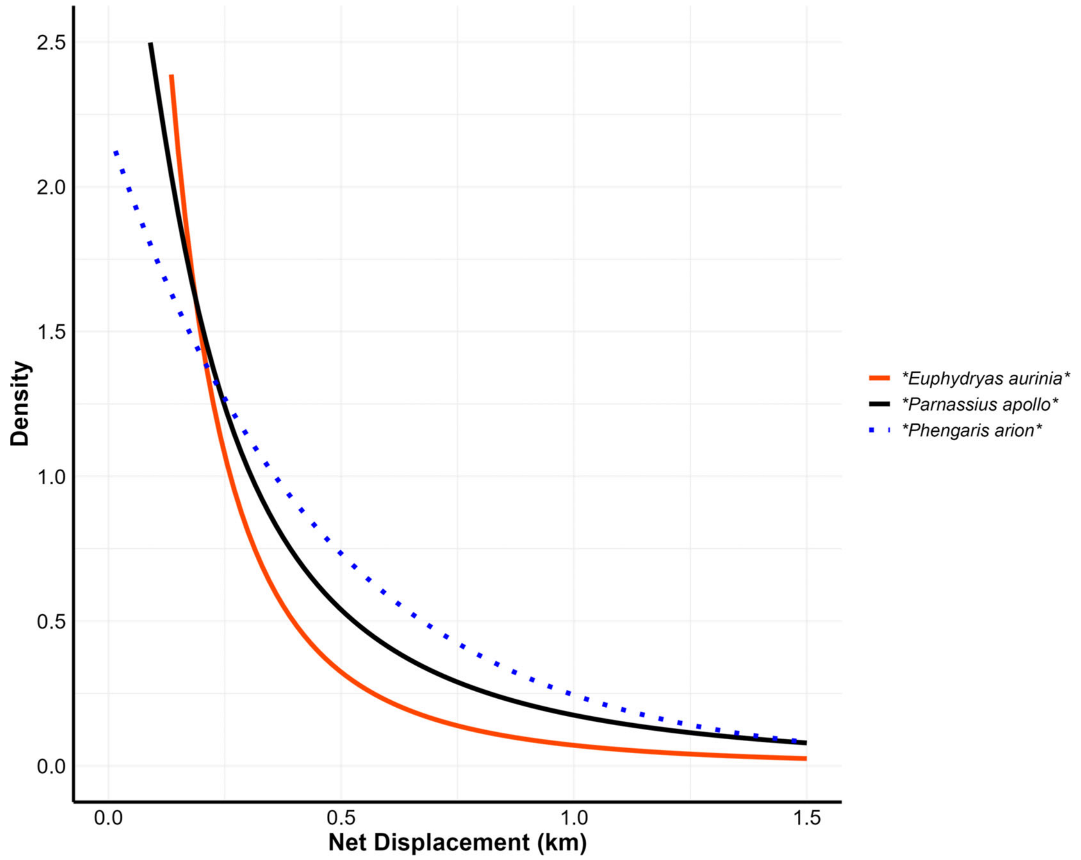

FIGURE 2 Best-fit dispersal kernels for net displacement of three butterfly species: *Euphydryas aurinia*, *Parnassius apollo* and *Phengaris arion*. Curves show the probability density (y-axis) across displacement distances in km (x-axis). Orange and black lines denote the lognormal fits for *E. aurinia* and *P. apollo*, respectively, while the dotted blue line denotes the exponential fit for *P. arion*. These models were selected based on minimum AIC (see Table S2 for model comparisons). Net displacement was calculated as the straight-line distance between first and last capture locations for each individual, ensuring statistical independence of observations.

TABLE 3 Estimated number of individuals (per 10,000) predicted to reach or exceed specific net displacement distances, based on each species' best-fit dispersal kernel.

Distance threshold	*E. aurinia* (per 10,000)	*P. apollo* (per 10,000)	*P. arion* (per 10,000)
≥0.1 km	5515	7644	8029
≥0.5 km	1191	2977	3337
≥1 km	406	1423	1114
≥5 km	11	101	0
≥10 km	1	21	0

Note: For *E. aurinia* and *P. apollo*, the lognormal model was used; for *P. arion*, the exponential model was used. (Values are rounded to the nearest whole number. 0 indicates an essentially zero probability at that distance for *P. arion*).

and the need to traverse unsuitable matrix quickly, a pattern commonly reported in butterfly movement ecology (Crone et al., 2019).

Dispersal kernel performance

Although a lognormal distribution provided a good fit for the movement data of *E. aurinia* and *P. apollo*, an exponential distribution fit *P. arion* best. This difference suggests that the underlying dispersal processes or movement tendencies may vary among the species. The exponential kernel for *P. arion* implies a higher likelihood of short movements and a rapidly declining probability of longer flights, consistent with the species' brief adult lifespan (only ∼2 days on average) (Franzén et al., 2024b; Osváth-Ferencz et al., 2017) and perhaps the mosaic of thyme and ant nest resources that keep most movements local. By contrast, the heavy-tailed lognormal distributions for *E. aurinia* and *P. apollo* capture the fact that while most individuals move short distances, a small fraction make very long flights (several kilometres or more). This finding is in line with our earlier work and with other studies showing that dispersal kernels can be species-specific (Nathan et al., 2012; van Langevelde & Wynhoff, 2009). Different statistical distributions often describe different species' movements best (Jordano, 2017), underlining that there is no one-size-fits-all model for butterfly dispersal. In our case, life history and behavioural traits likely play a role: *P. apollo*'s large size and soaring flight allow it to cover longer distances more frequently, whereas *P. arion*'s short adult life and urgent need to reproduce may curtail extensive wandering.

Cormack–Jolly–Seber (CJS) models separate apparent survival (φ) from recapture probability (p), allowing detection to be treated explicitly (Laake, 2013; Lebreton et al., 1992). Our estimated daily *p* values were similar across species (0.17–0.22), so variation in detection is expected to affect precision more than to bias interspecific contrasts in net displacement or kernel rankings under our one-value-per-individual design with year as a random effect. A possible exception is distance-dependent detection (e.g., long-distance movers being less likely to be recaptured), which would depress the upper tails; accordingly, tail probabilities should be interpreted as conservative. It is worth considering how sampling and detectability might influence these kernel estimates. We took care to standardise effort and found similar detection probabilities among species (∼17%–22%), suggesting that none of the species was dramatically more likely to be recaptured than the others. Still, *P. arion*'s low sample size (only 291 individuals with ≥2 captures) means its fitted distribution is based on fewer data points, potentially affecting the precision of the tail estimates. The lack of any predicted *P. arion* movements beyond 5 km (Table 3) likely reflects both biological reality and data limitation: even if a few individuals were capable of >5 km flights, our sample provides little power to detect such rare events. In contrast, our much larger samples for *E. aurinia* and *P. apollo* (thousands of individuals each) give us greater confidence that the lognormal tails for those species capture real long-distance dispersal tendencies. Overall, the use of net displacement and multi-year data provides a more robust picture of each species' dispersal kernel compared with earlier, shorter-term studies from smaller areas.

Rare dispersal events and their importance

While the majority of butterfly movements we recorded were local (within a few hundred metres), all three species demonstrated the capacity for rare but ecologically significant long-distance dispersal. We directly observed movements of up to ∼8–11 km, and our fitted kernels suggest that a very small percentage of individuals can go even farther (Table 3). Although only 3%–15% of individuals moved >1 km, such long-distance events are integral to metapopulation dynamics because they enable gene flow and colonisation of vacant habitats (Trakhtenbrot et al., 2005; Ugelvig et al., 2012). Our dispersal kernel extrapolations quantify just how rare these events are: on the order of one in a few hundred individuals for distances of several kilometres. For example, we expect roughly 1% of *P. apollo* to exceed 5 km, compared with about one-tenth of a percent of *E. aurinia*, and effectively none of *P. arion* (Table 3). These differences mirror the species' ecology. *Parnassius apollo* often inhabits extensive alvar and rocky outcrop systems and routinely flies long distances across them (Franzén et al., 2024b). *Euphydryas aurinia*, although generally tied to discrete fen or grassland patches, has shown the ability to recolonise across a network of meadows when habitat is available (Johansson et al., 2022; Zimmermann et al., 2011). And *P. arion*, despite traditionally being labelled sedentary, can disperse widely in continuous grassland landscapes (Simcox et al., 2024; Ugelvig et al., 2012) – though perhaps not to the extreme distances observed in *P. apollo*. Our results and these studies collectively indicate that butterflies often have a "hidden" dispersal potential that only becomes evident under suitable landscape configurations. Even species thought to be highly philopatric will take advantage of connectivity when it exists.

These rare long distance dispersers, though few in number, have disproportionate importance for long-term population viability. They are the individuals that can bridge distant habitat patches, rescuing declining populations or establishing new ones, and maintaining genetic diversity across the landscape (Hovestadt et al., 2011; Trakhtenbrot et al., 2005). Thus, from a conservation perspective, it is crucial not to ignore the tail of the dispersal distribution. Approaches like ours, which combine extensive field data with statistical models, help to illuminate that tail. However, we acknowledge that even eight years of CMR data might miss the most extreme dispersal events. Genetic methods (e.g. assignment tests or parentage analysis across widely separated sites) could complement our findings by detecting movements of individuals that were never observed in the field, thereby providing a fuller picture of landscape connectivity (De Ro et al., 2021; Ugelvig et al., 2012).

Implications for conservation and movement ecology

Our findings imply that these endangered butterflies may be more mobile and resilient to habitat fragmentation than previously assumed, provided that habitat quality is high or some habitat connectivity exists. The relatively high mobility of *P. apollo* and *P. arion* in Gotland suggests that conservation efforts for these species should consider landscape-level planning. Maintaining a network of habitat patches within a few kilometres of each other is likely beneficial, as a non-trivial fraction of individuals can move among patches at that scale. For *E. aurinia*, which showed more restricted movement, creating stepping stones or corridors might be necessary to facilitate dispersal between fens or meadows separated by more than 1–2 km. Importantly, the positive, albeit weak, displacement^2 ∼ time relationships we observed indicate that spatial spread does increase over time for all species, albeit slowly. This means that given enough time (and successive generations), populations can expand their range through a series of shorter moves, especially in heterogeneous landscapes that provide intermediate refuges. For instance, Johansson et al. (2020) observed that *E. aurinia* shifted its local distribution toward wetter areas following a drought, illustrating how individuals can redistribute in response to environmental changes if suitable microhabitats are accessible (Johansson et al., 2020). Larger, heterogeneous conservation areas can stabilise population fluctuations and buffer these butterflies against climate variability by offering alternative habitats within dispersal reach (Kindvall, 1996).

More generally, the deviation from simple diffusion and the use of heavy-tailed dispersal kernels both point to multiple movement behaviours operating at different scales. Within patches, butterflies engage in intensive search and exploitation (leading to subdiffusive movement), whereas between patches they switch to a ranging mode (more diffusive, directed movement). This reinforces the notion that movement ecology models and conservation plans should incorporate context-dependent behaviour (Jeltsch et al., 2013). Simple diffusion models may greatly underestimate dispersal distances if an organism's occasional long-range movements are not accounted for. Conversely, assuming too high a frequency of long-distance movement (e.g. using a broad exponential or normal kernel for a largely sedentary species) could overestimate landscape connectivity. Our comparative approach shows that even closely co-occurring species can differ in this regard; conservation strategies need to be tailored to each species' movement profile. For example, *P. apollo* might readily use a network of rock outcrops separated by several kilometres, whereas *E. aurinia* might require contiguous or closely spaced meadow habitat for persistence. Recognising these differences will help in designing reserves and corridors.

Limitations and future directions

A key limitation of our study is that net displacement provides only a minimum estimate of actual movement, since we do not track the full path between captures. If a butterfly meanders within a patch, our method underestimates the total distance it travels. This could particularly affect our interpretation of area-restricted search: an individual might roam extensively within a patch but still have a small net displacement. Developing methods to integrate such intra-patch movement (e.g. high-resolution GPS or harmonic radar tracking over short periods) would complement the CMR approach. Another limitation is that we did not explicitly separate movements occurring within habitat patches from those occurring between patches. Future work could incorporate detailed habitat data or GIS analyses to classify whether each observed movement stayed within suitable habitat or traversed the matrix (unsuitable habitat). It may also be useful to consider the shape and size of habitat patches when interpreting movement distances, since individuals often turn back upon reaching patch edges. Methods that simulate random movements confined within actual patch boundaries can provide a baseline for expected displacement distributions in the absence of between-patch dispersal (Hovestadt & Nowicki, 2008). Empirical evidence supports this idea – for example, Johansson et al. (2025) observed that marsh fritillaries were significantly less likely to cross from ungrazed, high-quality habitat into adjacent grazed, low-quality areas. Incorporating patch geometry and edge behaviour into movement analyses could thus help distinguish routine within-patch movements from true dispersal events, leading to more accurate interpretations of displacement data.

Our conservative use of only first-to-last capture distances (one per individual) likely underestimates total movement potential compared with summing all sequential moves. However, we chose this approach to avoid pseudoreplication and to reduce bias from highly mobile individuals being over-represented in the data. Interestingly, the mobility ranking we found among these species aligns with earlier studies on smaller spatial scales, suggesting that our conclusions are robust. In our analyses, we explicitly addressed potential pseudoreplication and detectability issues; this strengthens the validity of our interspecific comparisons. Nonetheless, continued methodological refinements and longer time series will help capture the full spectrum of butterfly dispersal and improve landscape-level conservation strategies.

CONCLUSION

By integrating eight years of mark–recapture data for three co-occurring threatened butterflies, this study provides a quantitative, comparative perspective on movement distances. We demonstrated clear differences among *E. aurinia*, *P. apollo* and *P. arion* in typical dispersal range and the frequency of long-distance movements. We also showed that all three species exhibit area-restricted movement rather than simple random diffusion. The use of net displacement data and appropriate dispersal kernels allowed us to estimate the probabilities of ecologically important dispersal events for each species. These findings refine our understanding of butterfly mobility and underscore that even "sedentary" species can disperse when habitat configuration permits. In practical terms, our results offer species-specific dispersal parameters that can inform the design of conservation networks – for instance, indicating how far apart habitat patches can be while still retaining connectivity. Ultimately, a better grasp of movement patterns in these butterflies will aid in developing effective management plans to ensure their long-term persistence in fragmented landscapes.

AUTHOR CONTRIBUTIONS

Markus Franzén: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision; resources. **Anders Forsman:** Conceptualization; funding acquisition; writing – original draft; methodology; visualization; writing – review and editing; supervision; resources. **Oskar Kindvall:** Conceptualization; data curation; supervision; methodology; writing – review and editing. **Victor Johansson:** 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 that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data is available at Figshare https://figshare.com/s/97f723d574c67008d41e.

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SUPPORTING INFORMATION

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

Data S1: Supporting Information

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