ORIGINAL ARTICLE

Restoration and rescue in an age of extinction: advances in arthropod reintroduction (and translocation)

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Rapid selection for increased dispersal rates by the endangered butterfly *Phengaris (Maculinea) arion* across restored landscapes

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Abstract

1. When designing restorations for durable metapopulations of endangered butterflies, it is important to understand how frequently the adults mix between sites and their probability of colonising vacant patches unassisted by human translocations.

2. We analysed 43 examples of natural dispersal by *Phengaris arion* L. to restored sites in three regions following its reintroduction after extinction to the UK. We compared the years taken to reach restored habitats with the distance from a source colony, the number and density of *P. arion* on source sites, the size of source sites, the nature of the intervening matrix, summer temperatures, the incidence of drought and whether a more dispersive phenotype has evolved across restored landscapes.

3. Isolation of sites was the most important constraint on the colonisation of new habitats, followed by the number, but not the density, of *P. arion* on source sites. Emigration was more frequent in warm summers and when the habitat was degraded by drought, but neither factor remained significant in multifactorial analyses. A matrix of woodland between sites was a greater barrier to dispersal than open or mixed terrain, but again insignificant in multifactorial analyses.

4. A more mobile phenotype of *P. arion* has evolved while it exploited vacant habitat patches during its first 10–12 generations in the UK. Adults now fly twice as far to find new colonies as in the early years. We map the probabilities of linking restored sites with neighbouring populations in three former landscapes in the Cotswold Hills of Gloucestershire, UK.

KEYWORDS
conservation, habitat quality, isolation, large blue, metapopulation, reintroduction, translocation

INTRODUCTION

Two factors are often cited as key drivers of the declines of butterflies in European and other temperate landscapes (Hanski, 1999; Thomas, 1984, 1991, 2016; Thomas et al., 2001, 2004; Warren et al., 2001, 2021). Changing land-use practices have destroyed, reduced or degraded the narrow niches occupied by the larvae of most species (Thomas, 2016; Thomas et al., 2011). Compounding this, about 75% of species live in predominantly closed populations (Thomas, 1984), with dispersal rates that may be too limited to exploit the fewer, ephemeral and increasingly isolated patches of new habitat as they arise within the seral stages of grasslands (Hanski, 1999; Thomas, 1983), woodlands (Warren, 1987), marshland and heath (Thomas et al., 1992).

In general, populations of local species evolve to be ever more sedentary as patches of breeding habitat become rarer and more isolated in landscapes (Baguette et al., 2003; Dempster et al., 1976; Maes & Van Dyck, 2022; Schtickzelle et al., 2006; Van Dyck & Matthysen, 1999). Conversely, there may be a selection for more dispersive phenotypes if additional patches become available (Dempster, 1991; Hill et al., 1999; Thomas, Hill, & Lewis, 1998). Knowledge of the mechanisms involved in butterflies derives largely from studies of 11 European species. Dempster (1991) showed that museum specimens of *Papilio machaon* and *Phengaris arion* possessed wider thoraxes—which house larger wing muscles—after periods of local expansion in the 19th and early 20th centuries, but the reverse during periods of decline: adult *P. machaon* with larger thoraxes were confirmed as stronger fliers, whilst Bonelli et al. (2013) reported dispersal depression in isolated populations of *P. arion*. Similar morphological changes have been found in expanding populations of *Hesperia comma* (Hill et al., 1999), *Pararge aegaria* (Thomas, Hill, & Lewis, 1998) and *Pieris* species (Dederichs et al., 2024), and in contracting ones of *Plebejus argus* (Hughes et al., 2003) and *Lycaena epixanthe* (Crawford et al., 2018). Various trade-offs are described in *P. aegaria* according to landscape structure and how the cost of evolving stronger wing muscles—and thus colonising distant sites more quickly—is balanced by lower fecundity compared with weaker flying individuals (Berwaerts et al., 2002; Hughes et al., 2004; Merckx & Van Dyck, 2006; Thomas, Hill, & Lewis, 1998). In Finland, Hanski (1999) and Niitepold et al. (2009) concluded that there was no such association between dispersal and morphology across *Melitaea cinxia* metapopulations, despite initial studies (Kuussaari et al., 1996). However, emigration decreased in cool summers; adults were also less likely to leave habitat patches that were large and contained high densities of the butterfly or many flowers. Those that did were significantly larger than the stay-at-homes and had enhanced expression of the *Pgi* gene, known for its association with dispersal in other insects (Niitepold et al., 2009).

In addition, Niitepold et al. (2009) found that adult *M. cInxia* were most dispersive at intermediate temperatures of 18–23°C, while females of *Euphydryas anicia* (Odendaal et al., 1989), *Proclossiana eunomia* (Baguette et al., 1998), *Phengaris teleius* and of *P. nausithous* (Nowicki & Vrabec, 2011) were more likely to emigrate from high-density patches due to harassment from males. Nowicki et al. (2014) found that the nature of the matrix between sites also influenced dispersal.

The re-establishment of *P. arion* to the UK, following national extinction in 1979, provides an opportunity to study not only the individual but also the collective processes influencing dispersal across three landscapes where its specialised habitat has been restored on >50 separate sites (Thomas et al., 2009, 2019). *P. arion* (until recently known as *Maculinea arion*) is an iconic species in conservation (Thomas & Settele, 2004), famed for its beauty, rarity and a highly specialised life-cycle that involves feeding briefly as a larva on the flowers of *Thymus* spp. or, on a few UK sites, *Origanum vulgare*, before entering a *Myrmica* ant nest, where it lives for 10–11 months and acquires >98% of its final biomass by eating ant brood (Thomas &

Wardlaw, 1992). In the case of *O. vulgare*, oviposition is biased towards individual plants that emit high levels of carvacrol, owing to their roots having been disturbed by *Myrmica* species of ant, which are more tolerant than other ant genera of this noxious volatile (Patricelli et al., 2015). Like other *Phengaris* species, *P. arion* employs a combination of chemical and acoustical mimicry to infiltrate and exploit a host ant society (Akino et al., 1999; Barbero, Bonelli, et al., 2009; Barbero, Thomas, et al., 2009; Nash et al., 2008; Thomas et al., 2013). In the UK and most of Europe, this specialisation restricts *P. arion* to sites where high densities of *Myrmica sabuleti* coexist with its initial foodplants (Tartally et al., 2019; Thomas et al., 1989, 2009).

P. arion is currently listed as 'Near Threatened' globally by IUCN (Gimenez Dixon, 1996) having previously been classed as 'Endangered', a designation to which it may revert should its status as a possible cryptic species in Europe and west Asia be confirmed (Meredith et al., 2024; Ugelvig, Vila, et al., 2011). Across Europe, *P. arion* is unequivocally an 'Endangered Species', having experienced >90% losses in 1990–2010 (van Swaay et al., 2010), with steep declines continuing (Osváth-Ferencz et al., 2017). The UK, however, provides an exception. There, bespoke regimes of grassland grazing, based on a detailed knowledge of its narrow larval niche, have enabled our definition of *P. arion*'s optimum habitat (>68% initial foodplants coexisting with fit colonies of *M. sabuleti*) to be restored to about 50 former sites and Protected Areas (Thomas et al., 2009, 2019). Following introductions of larvae from Sweden to Site X in Devonshire (1983–1985) and to Green Down in Somerset (1992; Figures 1 and 2), *P. arion* has flourished and spread naturally to most currently occupied sites, aided by occasional assisted translocations to new regions, landscapes or distant sites sourced from the burgeoning UK populations on Green Down, Collard and from FR (Figure 1) or from Daneway Banks in Gloucestershire (Thomas et al., 2019). Today (Figures 1 and 2) the species is well established in Somerset's Polden Hills and the Cotswold Hills of Gloucestershire, where the two largest populations each contain ∼9000 adults, an order of magnitude larger than those found in four central European nations; moreover, two other UK sites support densities roughly 25-fold greater than the highest reported elsewhere (Osváth-Ferencz et al., 2017).

Unlike the Levins-type ('Blinking Lights') metapopulations of *M. cinxia* (Hanski, 1999), *P. arion* and congeners exist as 'mainland-island' metapopulations, with the 'mainland' colonies being relatively long-lived (historically) and having low dispersal rates (Bonelli et al., 2013; Nowicki, Pępkowska, et al., 2005; Nowicki, Settele, et al., 2005; Osváth-Ferencz et al., 2017; Thomas, Clarke, et al., 1998). Here we draw upon 43 recorded instances of natural dispersal by female *P. arion* to restored sites in three separate regions of the UK since re-introduction from Sweden. We analyse the data to ask: (i) What is the probability of recently restored habitat patches being colonised naturally within UK restoration landscapes? (ii) Apart from isolation (distance), what other mechanisms affect colonisation rates? We consider both separately and in combination: (a) the nature of the matrix between sites; (b) the size of source populations; (c) the density of individuals on source sites; (d) the size (area) of source sites; (e) the incidence of summer drought (= temporary habitat degradation) prior
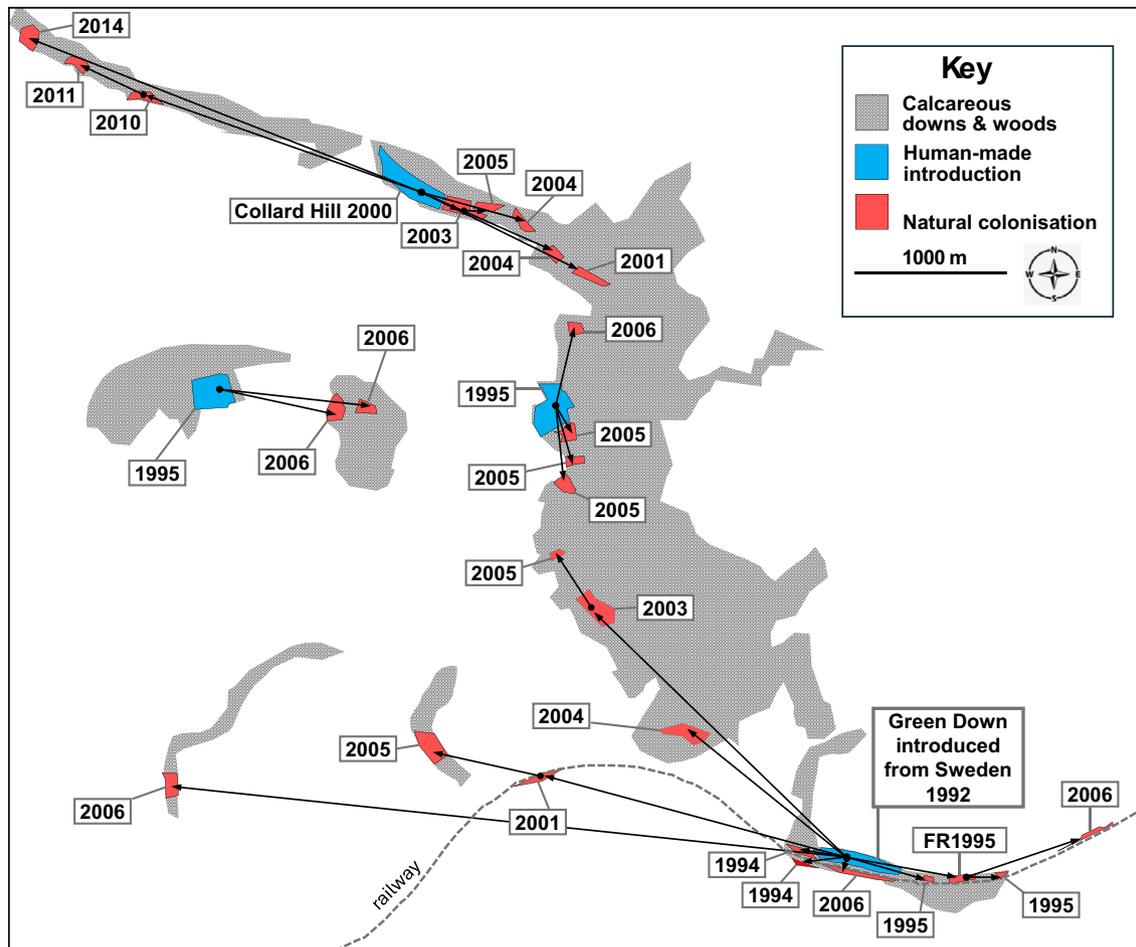
FIGURE 1 Recorded dispersal of *Phengaris arion* across the Poldens Hills landscape in Somerset in 1993–2023, following its introduction from Sweden to Green Down in 1992. Subsequent human-made introductions in this landscape used butterflies from Green Down and FR. Those to the Cotswolds were initially from Green Down, Collard Hill and FR.

to and during the adult flight period; (f) weather during the flight period; and (g) whether the creation of stepping-stones of new habitat patches across landscapes has led to the selection of more dispersive phenotypes, as suggested by Dempster (1991). If so, how quickly and to what extent does this evolve?

At a practical level, we consider whether natural dispersal is now sufficient to ensure the colonisation of newly restored sites, or to repopulate vacant patches of suitable but sub-optimal patches following local extinction after extreme, unfavourable or stochastic events? And beyond what distance are costly human-made translocations advisable rather than relying on natural spread to ensure colonisation within 10 years?

MATERIALS AND METHODS

Population estimates and location of new colonies

We performed no Mark-Release-Recapture (MRR) of adult *P. arion* during this study of dispersal in 1983–2023: thus, neither sex was

unnaturally disturbed during these studies. Instead, its eggs are conspicuous and can be easily found and accurately counted on *Thymus* flowerheads, giving total counts on small sites or estimates to within $\pm 10\%$ of population size by searching >100 1-m^2 random quadrats on larger sites (Thomas et al., 2009). Eggs on *Origanum* are less conspicuous but were counted easily enough on the three dispersal sites where this was the main foodplant. Since 1983, we also searched all available *Thymus* and sampled *Origanum* flowers on previously unoccupied sites that have progressively been restored to provide *P. arion* habitat (initial foodplant coinciding with >68% fit *M. sabuleti*) at multiple distances across landscapes on the edge of Dartmoor (1983–2004), in the Polden Hills of Somerset (1993–2014) and in Gloucestershire's Cotswold Hills (2011–2022). One example of our raw data, from Somerset, is displayed in Figure 1, which also shows where and when we made artificial introductions. Locations in the other regions remain confidential. In all but three instances, colony size and density of butterflies on the source sites were estimated every year using the aforementioned methodologies (Thomas et al., 2009).

We took the presence of one or more egg(s) as indicative of dispersal to a new site, although of 43 recorded 'colonisations', just five
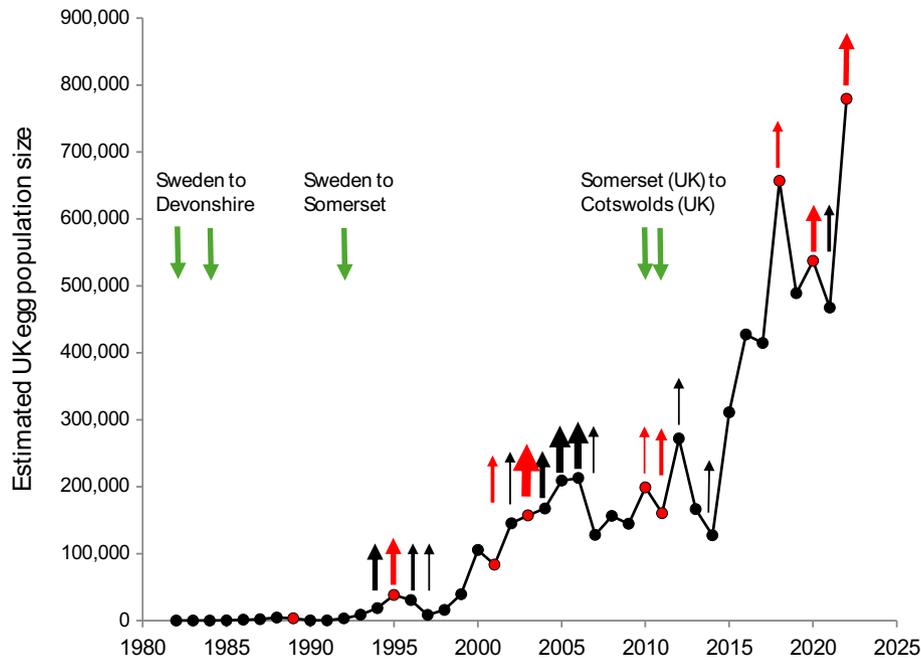
FIGURE 2 Combined size of the UK *Phengaris arion* populations (egg stage) since re-establishment from Sweden in 1983. Upward arrows indicate natural dispersal to new sites. Thickness of arrow indicates number of instances per year ranging from one (finest arrow) to seven (broadest arrow). Red arrows and markers indicate years of summer drought. Green downward arrows indicate translocations to UK regions directly from Sweden, or within the UK to the Cotswolds from populations that had bred for 18–19 generations in Somerset.

were based on a single egg (median = 9). All were fertile. This does not imply that a new colony was established immediately, although in over half the examples a population persisted for 7–28 generations (to date) after the first eggs were found (7 years' occupancy being the minimum for a re-introduced species to become subject to UK legal protection; also, the arbitrary number of generations in ecology taken by Pollard (1993) and Thomas et al. (2011) to distinguish between resident populations and ephemeral ones). Since mating generally occurs within 2 h of eclosion, sometimes before a female's wings have set, the remainder indicates that one or more mated females flew and bred there, laying a potential second generation.

Definition of a demographically distinct population

The definition of what constitutes a single habitat patch, or multiple separate ones, can profoundly influence analyses of the relative importance of isolation and site size in the exchange of individuals across metapopulations (Thomas et al., 2001). Based on our 1972–1978 MRR data and egg distributions, we defined a discrete site as any patch of suitable habitat separated from a source colony by >67 m of uninhabitable terrain (Thomas et al., 2009). That is more than double the minimum distance across the matrix used in most meta-population analyses of predominantly colonial butterfly species (e.g., Hanski, 1999; pers. comm.), but similar to that used in earlier studies of *Lysandra bellargus* and *Thymelicus acteon* (Thomas et al., 2001) and of *Phengaris nausithous* and *P. teleius* (Nowicki et al., 2014). In practice, only one out of 43 recorded *P. arion*

dispersals to a new habitat patch was within 100 m of the nearest source, and only nine were <250 m away. But to test for site independence, annual population dynamics were compared on the two closest sites to Green Down, including the one example of a colonisation <100 m from its source (Figure S1). Neither was synchronised with fluctuations on Green Down apart from a common crash in the great drought of 2014: we conclude that all three, and more distant sites, supported demographically independent populations.

Nature of the matrix between sites

Most meta-population models assume the matrix between sites is constant. However, Nowicki et al. (2014) showed that woodland was a greater barrier to emigration by *P. nausithous* and *P. teleius* than was open terrain, although individuals flew roughly twice as far when they did cross wooded landscapes. Here, we classed the matrix between each dispersal event into one of three categories: >80% 'open' ground (like *P. arion* habitat); 'mixed' terrain with 20%–67% woodland; or mainly (>67%) 'woodland'.

Identifying the source of new colonisations

We cannot be certain that we identified the exact source colony in every case, but we are confident that we did sufficiently often for any factors that influence dispersal to emerge. To test for bias, we classed

each designated source into one of three categories: 'Certain', for example after making assisted introductions to distant regions or new landscapes >7 km from any existing population, 'highly probable' or 'likely'. We present separate analyses for these subsets of likelihood in Table S1.

Distance

We measured the distance traversed to reach new habitat patches as the linear distance between the nearest points on the source and recipient sites. In analyses, we used untransformed measurements, since log values explained very similar (but slightly less) variance and distance squared significantly less.

Weather

Summer drought—sufficient to crisp the leaves of most deep-rooted nectar sources such as *Lotus corniculatus* and to reduce flowering in the more resilient *Thymus*—was indirectly measured by using UK Meteorological Office MORECS data of local monthly Soil Water Deficits (SWDs). Combined values of >280 SWD in May–July were taken to indicate severe drought during the flight period (Figure 2, which also displays the total size of the UK Large blue population each year and the incidence of recorded migrations). 'Drought years' were validated in the field. In addition, we compared both the incidence of dispersal and the distance moved with mean and mean maximum June temperatures obtained from local meteorological stations.

Statistical analyses

Statistical analyses were made using Minitab Statistical Software version 22. For seven individual parameters, we initially compared linear and quadratic regression models to explore associations between the distances traversed and each putative factor: time before colonisation occurred, the number of *P. arion* in source colonies, the density of *P. arion* in source colonies, the physical size (area) of source sites, summer temperatures, testing selection for a more dispersive phenotype, and for asynchrony in population fluctuations on neighbouring sites (Figure S1). In all cases, linear models explained much greater variance between data than quadratic ones and were used in subsequent analyses. For two other parameters, the composition of the matrix and the incidence of summer drought, sample sizes in one category were small, so comparisons were made using Mann–Whitney tests. Finally, an analysis of variance (ANOVA) general linear model (GLM) was employed to determine the relative importance of five factors that were individually correlated or associated with variation in dispersal, plus adult density on source sites, which had been expected to be influential.

RESULTS

We recorded 43 examples of adult female *P. arion* ovipositing on new sites in 19 of the 30 years after 1992, when larvae were introduced from Sweden to Somerset after 150 years' absence (Figure 2). In 40 cases, we also measured population size on the source site in the year of dispersal. Below we consider the possible influence of the eight parameters that may have influenced dispersal, first individually then in multifactorial analyses.

Weather effects (i) drought

Nine summer flight periods experienced such extreme summer drought ($\sum$May–July SWD >280) that the vegetation was scorched and both *Thymus* and other nectar sources were greatly diminished (Figure 2). We found some evidence that dispersal to new sites was more frequent in years of summer drought, with an average of 1.03 ± 0.33 SE events per year in non-drought years compared with 2.78 ± 0.70 SE events during summer droughts. This suggests that females are more than twice as likely to leave source sites when their surroundings have withered. Despite the low incidence of summer drought, the significance of the difference is sufficient to include in later multi-factorial analyses (Mann–Whitney: $N = 9$, 31; medians = 3, 0; $W = 262$; $p_{adj\ for\ ties} = 0.007$; $p_{not\ adj} = 0.013$).

Weather effects (ii) June daytime temperatures

The incidence of females dispersing from an established colony was greater the warmer the year ($R^2_{adj} = 10.6$, $N = 29$, $p = 0.048$), but the putative association was weaker than that with summer drought. Nor did it remain significant when extreme drought years were omitted ($N = 24$, $p = 0.06$). For all years, the distance travelled to a new site showed no correlation or relationship with June daytime temperatures ($p = 0.89$, $R^2_{adj} = 0$). This parameter was therefore omitted from later analyses.

Influence of the matrix between sites

We found no difference between the rates at which *P. arion* dispersed across terrain consisting of open or of mixed habitat, or of the distance achieved (Table 1). However, the few matrixes dominated by woodland provided a significantly greater barrier to the rate of dispersal, and marginally significant shorter distances were traversed when this did occur, at least compared with matrixes of mixed habitat.

Density of butterflies and size of source sites

There was no correlation between the density of *P. arion* per m² on each source site with the distance traversed or the years that elapsed

TABLE 1   Influence of the matrix on dispersal by *Phengaris arion*.

Rate of spread	Mean (median) m. traversed per year	SE	N	Mann–Whitney W-value	p	Mann–Whitney W-value	p
Open habitat	244 (218.2)	41	17	295	ns		
Mixed habitat	220 (218.1)	33	17			258	ns
Woodland	104 (92.0)	29	8	264	0.013		

Total distance dispersed	Mean (median) m. traversed	SE	N	Mann–Whitney W-value	p	Mann–Whitney W-value	p
Open habitat	918 (287)	264	17	255	ns		
Mixed habitat	1412 (987)	316	17	256	0.045	215	ns
Woodland	374 (339)	59	8				

to reach a new site ($R^2_{adj} = 0$). Subsamples of the data gave the same result when analyses were confined to sources identified as being 'Certain' or 'Certain and Highly Probable' (Table S1).

Size (area) of a source site

Nor was there any correlation between the size of a source site and the years that elapsed before females reached a new site ($R^2 = 1.4\%$, $N = 39$, $p = 0.47$). As it is related to butterfly density, this parameter was excluded from later analyses.

Total number of butterflies on source sites

As expected, there was a strong positive correlation between the absolute number of *P. arion* in source populations and the distances crossed to reach each new patch (Figure 3a, $R^2 = 40.5\%$, $p < 0.001$). Subsamples of the data showed a reduced, but still significant, correlation with *P. arion* numbers when analyses were restricted to sources classed as 'Certain' or 'Certain + Highly Probable' (Table S1). Although some, but not all, examples of which we were least or less certain involved some of the longer distances traversed, this may also indicate some bias in favour of high numbers when we identified the source site.

Isolation: Distances crossed and the years taken to reach new habitat patches

Much the strongest single-factor correlation found was between the distance a new patch was located from a source and the years that elapsed before it was reached (Figure 3b, $R^2 = 65.3\%$, $p = 0.0000$). Subsamples of the data again gave slightly weaker correlations when confined to sources identified as 'Certain' or 'Certain + Highly Probable', but the reduction was substantially

less than in the case of the population size on source sites (Table S1).

Has there been selection for a more dispersive phenotype as populations spread?

In Figure 3b, the correlation ($R^2 = 72\%$) between the years that *P. arion* took to colonise a new site and the distance each was located from its source was yet closer ($R^2_{GLM} = 87.7\%$) when dispersal after the first 12 generations following introduction from Sweden was classed separately from data from the initial years. The intercepts (Constants $= -8.0$, -146.1, respectively) of the two regressions differ at $p = 0.005$, and their slopes at $p = <0.001$, suggesting that distances traversed in the early years were significantly shorter, and colonisation took longer to achieve, than in 2005–2022.

A more complex pattern emerges in Figure 3c when the rate of spread (distance traversed/years before a new site was 'colonised') is compared with the calendar years in which dispersal occurred. Again, there was a rapid increase in dispersal rates in the early generations after Swedish butterflies were introduced followed by much variation and near flat-lining after 2004. However, some seemingly anomalous short-distance data points in recent years are explained by the creation of new habitat that was previously unavailable near an established colony or was due to more recent translocations to distant sites, which then rapidly colonised nearby patches. For example, the four colonisations in 2022 (Figure 3c) were all within 200 m of an introduction to a new landscape made in 2020. Nevertheless, a consistent pattern emerges of increasing dispersal rates over the years; however, we analyse subsets of these data, apart from post-2004 on all sites including data from 2022 (Table 2).

To summarise, taking 2004–2005 as a cut-off after which there was little, if any, increase in dispersal rates, it transpires that females were flying twice as far to reach new sites in the second (2005–2022) phase of colonisation than in the first, on average 258.0 ± 29 SE m per year compared with 131.3 ± 17 SE m per year, respectively
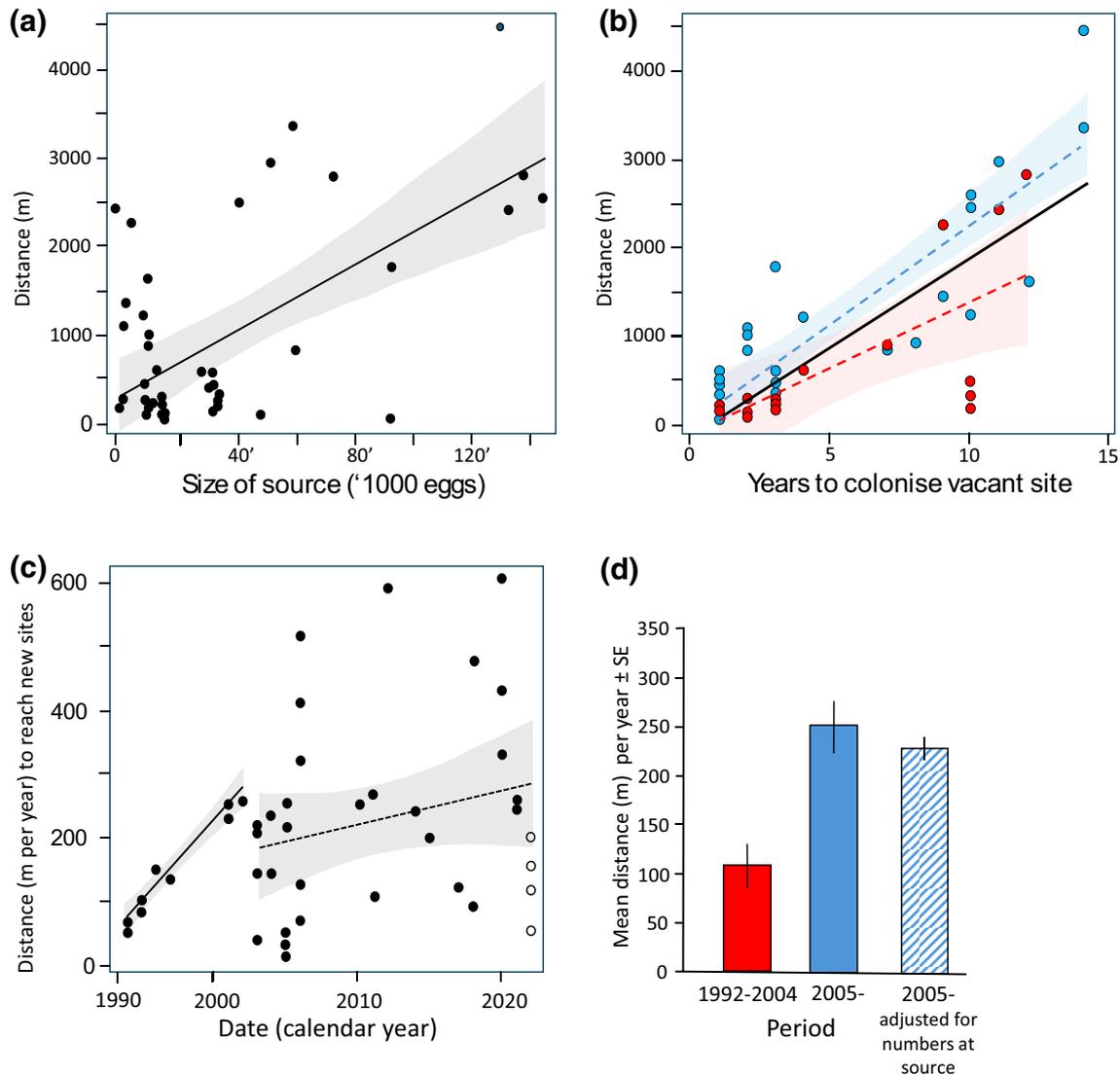
INCREASING DISPERSAL IN *PHENGARIS ARION*

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FIGURE 3 Distances flown by emigrants to reach a vacant new site compared with: (a) the number present on each source site ($R^2 = 40.5\%$, $N = 38$, $p < 0.0001$, shading = 95% CI); (b) the time (years) taken to reach it (black regression line, $R^2_{all\ years} = 72.1\%$, $p < 0.0001$, $N = 41$). Red markers = dispersals in the first 12 years after introduction of the Swedish genotype to the UK; Blue = subsequent years (2005–2022). Shading = 95% CI (c) The rate of spread (distance flown to reach a new site/years before it was colonised) compared with the calendar year when each migration occurred; open circles indicate habitat unsuitable before 2022. Shading for pre- and post-2004 regressions = 95% CI. (d) The average distance colonised per year in the first 12 years after introduction from Sweden (red), and after 13 or more generations in the UK (blue; 2005–2022). The hatched blue column shows the 2005–2022 rate of spread adjusted for the slightly higher number of individuals on source populations post-2004.

(Figure 3d, 2-sample $T_{11} = -3.8$, $p = <0.0001$). Despite the increase in total UK *P. arion* numbers (Figure 2), the increase in recent vagility is only slightly reduced to 249.3 ± 28 m per year in 2005–2022 when adjusted for the number of *P. arion* flying on source colonies during each period (Figure 3d). This is because the average number of butterflies on source sites was very similar in the two periods, measuring 33,348 ± 11,638 SE eggs per source in the first 12 years and 34,561 ± 5818 SE eggs in 2005–2022. This difference is statistically trivial (two-sample $T_{21} = -0.09$, $p = 0.97$), nevertheless, we further adjusted for source numbers in Figure 3d (blue hatched column) and in models of metapopulations (Figure 4).

Multifactorial analyses

Five factors showed significant associations with *P. arion* dispersal when considered in isolation: summer drought, numbers on source colonies, isolation of (distance from) new sites and increasing dispersal rates during the first 12 generations after translocation from Sweden. In Table 3, we examine the relative impact of them all combined; we also include *P. arion* densities on source sites, which was a stimulus for emigration in three previous studies of butterfly dispersal (Baguette et al., 1998; Nowicki & Vrabec, 2011; Odendaal et al., 1989).

TABLE 2 Comparisons of mean distances traversed per year (Figure 3c) for different periods since 1992 ± inclusion of data for 2022 when new habitat close to two sources first became available.

Period	Correlation with mean distance per year		
	R^2	p	N
All (1992–2022)	11.1	0.031	42
All 1992–2021 (omits 2022)	19.1	<0.005	39
Somerset only (Figure 1, 1992–2014)	27.1	0.005	27
First 12 years (Somerset only) from Sweden	95.8	<0.0001	8
Post-2004 (2005–2022)	4.1	0.253 ns	34
Post-2004 (2005–2021, omits 2022)	15.6	0.031	30

Taken together, ANOVA shows that the isolation (distance) of unoccupied habitat from a source colony of *P. arion* still explains most of the observed variation in the years that elapsed before a female reached it. Population size on source sites also explained a significant amount of variance but note that this may have been overestimated due to bias in identifying the relatively few sites where the location was less certain (Table S1). Entering pre-2005 and 2005–2022 colonisations as separate cohorts (Figure 3b,d) again showed a significantly greater rate of colonisation rates during the latter years when all other factors are accounted for.

In contrast, the incidence of drought and the composition of the matrix, which showed weaker individual associations with dispersal, were no longer significant in explaining overall rates of spread. Nor, as expected, did the density of butterflies on each source sites.

DISCUSSION AND CONCLUSIONS FOR CONSERVATION

Butterfly dispersal

This study is unusual in that we could quantify and compare the individual and collective roles of eight factors that might influence the rate of spread by a colonial butterfly from established populations to vacant habitat patches. Our results confirm the influence of several but not all the parameters found to affect other species in other landscapes. They indicate that three determinants (distance, numbers on source populations, evolution of a more dispersive phenotype) rendered the five other mechanisms insignificant in the overall spread of *P. arion* in the UK, even though three of the latter registered significance in isolation.

Our most surprising result was that dispersal by female *P. arion* was not even weakly correlated with the density of adults on source sites, despite two UK source populations existing at 25 times higher densities than those known in central Europe (Osváth-Ferencz et al., 2017). This contrasts with work on five other butterflies living in either Levins (Niitepold et al., 2009; Odendaal et al., 1989) or mainland-island metapopulations (Baguette et al., 1998; Nowicki &

Vrabec, 2011). Our landscapes were perhaps unusual in that there was no correlation between the number and the density of butterflies on individual source sites ($R^2 = 8.1\%$, $p = 0.08$), which allowed us to compare each parameter separately as well as together. Although Baguette et al. (1998), Niitepold et al. (2009) and Nowicki and Vrabec (2011) cite male harassment of females as driving emigration from high-density populations in four species, including in two other *Phengaris*, we have not observed this in our (undisturbed) *P. arion* populations. We also note that the highest densities of adult *P. arion* are invariably supported by sites with the highest quality of habitat for larval survival, a parameter that varies by ~75-fold between suboptimal (but just suitable) and optimal habitat (Thomas et al., 2009, 2011). A reluctance to quit high-quality habitat possibly explains our result.

The influence of the matrix between adjacent habitat patches was well studied by Nowicki et al. (2014) on two other species of *Phengaris*. For *P. arion*, we likewise found that predominantly wooded landscapes provided an obstacle to dispersal, but in its case the individuals that did cross woodland achieved shorter distances than when crossing other matrixes, the opposite to Nowicki et al.'s (2014) result. Our sample size (8) is too small to be conclusive concerning wooded matrixes, which may prove to be more influential in other landscapes.

Climate warming has not increased the incidence of summer droughts in southern England during the past three decades (Figure 2), in contrast to its severe impacts on larval survival while exploiting ants in other months (Thomas et al., 2009). Our results suggest a rough doubling of emigration when desiccation dramatically reduced nectar availability, but this occurred too seldom to influence metapopulation dynamics over 3–4 decades (Table 3).

Like other authors (Dederichs et al., 2024; Dempster, 1991; Dempster et al., 1976; Hill et al., 1999; Thomas, Hill, & Lewis, 1998), we conclude that *P. arion* has experienced strong and rapid selection for a more dispersive phenotype after just 10–12 generations of spreading between restored patches of habitat, as predicted by Dempster (1991; pers. comm.). This makes the colonisation of a new site roughly twice as likely compared with the original introductions from Sweden. With UK metapopulations still expanding, we have yet to record any reversal of this trait. Nor have we data to explore whether the evolution of a more dispersive phenotype occurred at the cost of reduced fecundity, as in *Pararge aegeria* (Berwaerts et al., 2002; Hughes et al., 2004; Merckx & Van Dyck, 2006; Thomas, Hill, & Lewis, 1998). We simply note that the average population increase (λ) over the first three generations of growth on restored sites has been the same whether a new site was colonised by the initial Swedish phenotype ($\lambda = 6.30 \pm 3.1$ SE, $N = 7$) or by post-2004 individuals ($\lambda = 6.62 \pm 3.0$ SE, $N = 7$; Mann–Whitney, ns at $p = 0.609$). Both values demonstrate the adaptive advantage of colonising an unoccupied habitat patch. In contrast, the annual value of population change stabilises at around 1 in long-established populations (e.g., Figure S1: $\lambda_{Green\ Down} = 1.079$; $\lambda_{Near\ Rail} = 0.950$; $\lambda_{New\ Embankment} = 0.985$) due to high density-dependent larval mortalities caused by starvation in overcrowded *M. sabuleti* nests (Thomas et al., 2009; Thomas, Clarke, et al., 1998; Thomas & Wardlaw, 1992).
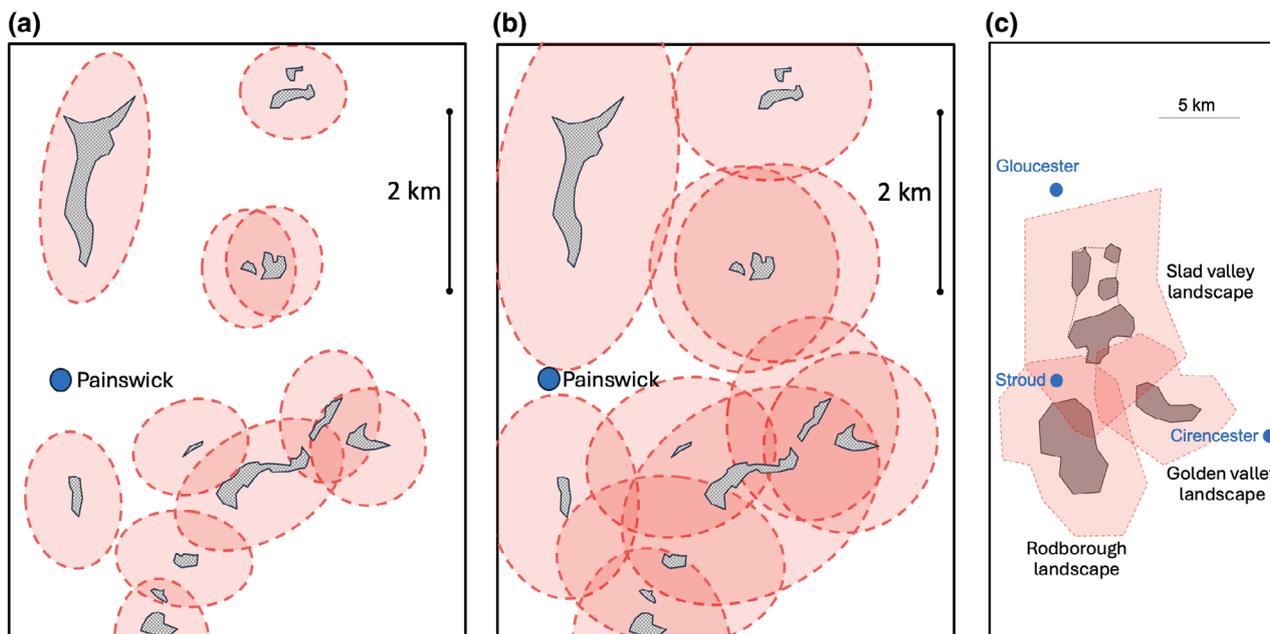
INCREASING DISPERSAL IN *PHENGARIS ARION*

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FIGURE 4 Average dispersal ranges, assuming complete habitat restoration, by one or more emigrant *Phengaris arion* over a 5-year period in the Slad Valley landscape, a former stronghold in the Cotswolds Hills, Gloucestershire, UK. (a) Average range of females originally imported from Sweden between habitat patches (light grey stipple). (b) Average range after evolving a more dispersive phenotype in Somerset in 1994–2022. (c) The three isolated historical landscapes for *P. arion* metapopulations in the Cotswolds based on Swedish phenotypes (dark grey), showing how these are predicted merge into one super-metapopulation at least once every 10 years due to the increased mobility of current individuals (red shading).

TABLE 3 ANOVA general linear model of six parameters compared with the years taken by *Phengaris arion* to reach new sites ($N = 39$, $S = 1.850$, $R^2 = 84.8\%$, $R^2_{adj} = 8.9\%$, $R^2_{pred} = 78.3\%$).

Factor	DF	ANOVA	
		F-statistic	*p*
Distance	1	110.17	0.000
Number on source site	1	5.69	0.023
Density of source site	1	1.51	0.228 ns
Drought	1	0.71	0.407 ns
Matrix (open, mixed, wood)	1	0.04	0.839 ns
Swedish or post-2004 phenotype	1	9.69	0.004

Abbreviation: ANOVA, analysis of variance.

Conservation

We hoped to answer three practical questions concerning the conservation of this endangered species: (i) Are new populations on restored habitat patches sufficiently interconnected to maintain viable metapopulation dynamics across a landscape? (ii) Is sufficient genetic diversity likely to be achieved by relying on natural colony foundation involving one or a few females? Will it be enhanced or maintained by subsequent exchanges between populations? (iii) When is it prudent to make expensive human-assisted translocations rather than rely on natural colonisation? For despite the welcome increase in vagility, *P. arion* remains a sedentary butterfly in the UK, with similar powers

of dispersal to *Mellicta athalia* (Warren, 1987), though nowadays greater than *Satyrium pruni* or *P. argus* (Thomas et al., 1992).

Our results appear to satisfy the first question. Current dispersal rates suggest that, once initially occupied, individual populations of *P. arion* will now remain interconnected within each of its former landscapes in the Cotswolds (Figure 4) and in Somerset (Figure 1), at least to the extent of one or more females moving between adjacent sites up to five times once every 5 years, so long as potential and former sites are suitably restored. We give illustrative projections for the classic Slad Valley landscape in Gloucestershire, first assuming the dispersal rates of the original Swedish phenotype (Figure 4a), then the more dispersive current one (Figure 4b). Dispersal will also be enhanced if optimal habitat, supporting populations of 1000–10,000 adults, is created, as has already been achieved on six sites in the Cotswolds and on four of the more clustered colonies in Somerset. Moreover, the three historical landscapes of Gloucestershire could themselves now become inter-connected, forming a super-metapopulation across the Cotswold Hills (Figure 4c).

Genetic implications of natural colonisation or human-assisted translocations

All current populations of *P. arion* in the UK are descended from the translocation to Green Down of 281 final instar larvae collected in 1992 from 11 sub-populations in Öland, Sweden; few were likely to be siblings (Meredith et al., 2024). Ten generations later, Andersen

et al. ([2014](#)) showed that three UK colonies within 1 km of Green Down had maintained similar diversity to their Swedish source, but that two others, 6.4 and 3.4 km away, were somewhat, but not seriously, impoverished. Ugelvig, Nielsen, et al. ([2011](#)) found that surviving *P. arion* populations in Sweden were fit, with relatively high genetic diversity for the species, and concluded that there was sufficient gene flow for metapopulations to remain fully functional if populations were separated by no more than 10 km. By contrast, a small population in Denmark, completely isolated for decades, had experienced genetic erosion: nevertheless, Ugelvig et al. ([2012](#)) concluded that their '*results suggest that M. arion is less sensitive to genetic erosion via population bottlenecks than previously thought, and that managing clusters of high quality habitat may be key for long-term conservation*'.

Since we have only once recorded dispersal to a new site that was >4 km from the nearest source (Figure [3b](#)), we assume that more distant natural colony foundations emanate from a single, or very few, females, and will also be liable to local extinction through stochastic events during the first 1–5 generations (Thomas et al., [2011](#)). We, therefore, consider it prudent to continue to translocate 300–500 final instar larvae, lab-reared from eggs collected on different dates from more than one source, to restored habitat patches located >2 km from a source, despite the cost and despite Ugelvig, Nielsen, et al.'s ([2011](#)) more optimistic results.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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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. The comparisons made in Figure 3 a, b repeated for: (i) all data on the identity of source sites (Figure 1); (ii) a subset of data where the identity of each source site is certain or highly probable; and (iii) those where the source site is certain.

Figure S1. Annual fluctuations and trends are not correlated on the two nearest colonies to Green Down.

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