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The importance of unique populations for conservation: the case of the Great Orme's Head grayling butterfly *Hipparchia semele* (Linnaeus, 1758) (Lepidoptera: Satyrinae)

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Abstract

Small populations with unusual characteristics subject to extreme conditions provide opportunities for exploring adaptability in the face of environmental changes. Two sets of data have been examined to determine how unusual is the population of *Hipparchia semele* on the Great Orme's Head, North Wales, compared with other sites in the UK. The population on the Great Orme is shown to have unique features, including significantly reduced wing expanse and wing ocellation and extreme flight period characteristics. Analyses of flight period data from the UK Butterfly Monitoring Scheme (UKBMS) using over a hundred sites reveals that, although the Great Orme population is one of a number of sites from the Channel Islands to northern Scotland with an early mean flight period, it has by far the earliest flight period and longest flight period of all populations - the latter raising the mean flight period date. Furthermore the unique characteristics of *H. semele* on the Orme may well be underestimated, inasmuch as sampling of individuals for the phenotype study is incomplete, including only the area along the North Wales coast into Cheshire, while the UKBMS transect is restricted to the south-west portion of the headland. Unique populations are often accorded focused conservation effort; especially potential flagship species in decline as in the case of British *H. semele*. As the Great Orme population presents a rare opportunity for studying adaptations in an extreme local environment, particularly considering current projections for climate changes, we advocate further research and attention being given to this unusual population.

Keywords Adaptation · Climate · Flight period · Phenology · Phenotype · Wing expanse · Wing ocellation.

Introduction

Considering the plight of species in current modern landscapes subject to the exponential rise in human pressures, conserving individual populations has become an expensive undertaking. Even so, there is a powerful argument for special treatment for species and populations with unusual traits and genotypes. Spatially restricted populations form potentially valuable targets as evolutionary model systems, especially when they display unusual or rare phenotypes and genetic markers. They allow us to investigate adaptational bounds and the reasons underlying evolutionary changes. In butterflies phenotypic changes can be very rapid as, for instance, changes in wing patterns in introduced populations (e.g., *Plebejus argus*; Dennis, 1977) and populations experiencing range expansions (e.g., Japanese *Zizeeria maha*; Otaki et al. 2010). The fact that evolutionary changes can be rapid is an important counter to both stressful conditions (e.g., habitat loss) and a boon for evolutionary opportunities presented by expanding resource opportunities (Hoffmann and Sgro, 2011; Hill et al. 2011; Parmesan et al. 2015). Small unusual populations then, provide valuable testing grounds for adaptability in the face of change; butterfly species with highly varied responses in phenology and wing phenotypes to environmental gradients are particularly useful organisms for such research.

Unusual populations of two butterfly species (the silver-studded blue, *Plebejus argus*; and the grayling, *Hipparchia semele*) occupy the Great Orme in North Wales, an isolated peninsula and fossil island (Dennis and Hardy, 2018); both were described as subspecies by Thompson (1941; 1944). They were further described by Dennis (1977) and argued to be the product of current (Holocene) environmental selection regimes rather than the product of glacial refugia, the latter reconstruction suggested by Beirne (1947). It is clear that both populations consist of smaller individuals, and that they emerge earlier than those of the same species elsewhere along the North Wales coastline. *P. argus* has been studied intensively by C.D. Thomas and his research team, and consequently details of the life history and changes in the distribution of the species on the headland have been greatly enhanced (Thomas 1985a, b; Thomas et al. 1999, 2002; Dennis 2004; Dennis and Sparks, 2006).

A question still remains as to the flight emergence features of the population of *H. semele* on the Great Orme, particularly how early and extended it is compared to those of populations occurring along the North Wales coastline. Dennis (1977) was unable to study the butterfly during the earliest part of its flight period (early June) between 1968 and 1972, but he was aware that the butterfly lingered on the Orme into August. The objective of the current study is to examine the flight period of the population of *H. semele* on the Great Orme and compare it with populations elsewhere in the U.K. At the same time, the phenotype of the Great Orme population is compared with those of populations elsewhere along the North Wales coastline.

The grayling butterfly on Great Orme's Head provides a valuable study system for several reasons. It is an unusual species from the vantage of phenology, as in other respects (i.e., basking mode and defences against predators, Dapporto et al. 2019). *H. semele* is only one of two species flying earlier in the west (Roy and Asher 2003) and only one of three species not flying later in the cooler parts of its range (Roy et al. 2015). Roy et al. (ibid) also showed that for most species, the rates of flight period delay per degree Celsius over space were less than rates of delay over time (in cooler years), suggesting local adaptation in phenology. Thus *H. semele* on the Great Orme is an ideal candidate for testing local adaptation of phenology to climate variables; the headland is on the west side of the UK mainland, projects north into the Irish Sea and is surrounded by sea on all sides but for the narrow tombolo of Llandudno.

Methods

Wing expanse and wing spot size assessment

The study species *H. semele* is a widespread European species, but regarded as in the high risk category in the face of projected climatic changes (Settele et al. 2008). It is currently undergoing rapid decline in the UK (1976 to 2014; occurrence change: -62%; abundance change: -58%) and is a Biodiversity Action Plan Priority species (Fox et al. 2015). It occupies dry or rapidly draining largely coastal biotopes (steep limestone slopes, crags and sand dunes) in the UK (Table 1) and feeds on fine grasses, overwintering in the third larval instar. It is a prime model species for the study of mate location behaviour and bird predation in relationship to wing features such as marginal ocellation (Tinbergen, 1972; Dapporto et al. 2019).

Data for wing expanse (mid thorax to wing apex x 2 (mm)) and wing ocelli size (inter-neural measurement of the dorsal and ventral apical and anal wing ocelli (mm)) were obtained from 1968 to 1973 (Dennis 1977) and included 820 individuals from 15 populations in North Wales and Cheshire (Table 1, see Fig. 1 for sites). Differences between populations were calculated using ANOVA; both features were normally distributed and untransformed. Wing expanse for the Great Orme population was also investigated for change over the flight period (days; day 1 = June 1st).

Assessment of flight period

Flight periods were assessed from daily counts of butterflies obtained from the UK Butterfly Monitoring Scheme (UKBMS). The detailed methodology of the UKBMS is described by Pollard and Yates (1993). Briefly, at each site, a fixed route (transect) is walked in each of 26 recording weeks from 1 April (week 1) to 29 September (week 26), provided that weather conditions meet set criteria and volunteers are able to carry out a transect walk. Each transect is divided into sections (15 on the Great Orme transect) distinguished by biotope. All butterflies seen within fixed limits are recorded for each section and summed for the transect. We used weekly count data for the period 1976-2012. Initial data on *H. semele* were available from 318 sites (a site is regarded as a named location having a distinct transect route and location code) distributed across the UK, including the Great Orme. These data were filtered as noted below for suitable cover of recording weeks, number of years and period (years) of observations (sites in Fig. 2).

Calculation of flight period measures

Several measures were obtained to investigate the timing of the flight period, including the week of first appearance (variable WEEKmin) and final week (variable WEEKmax) of the flight period in any year, the length of the flight period (variable WEEKrange: maximum – minimum weeks), the mean flight week (variable WEEKmean) and accompanying statistics for variation, or span, of flight period (standard error for the calculation of the coefficient of variation, variable WEEKcv). The mean date of the flight period at any location and year was also measured as the weighted mean date of counts over weeks (variables wWKmean and its measure of variation, variable wWKcv); this gives an estimation of the date of mean abundance in the adult flight period (Brakefield 1987). To ensure a robust measure of flight dates, the data were filtered to ensure that at least 5 years' data were available for at least 5 weeks in each year for any given site. This reduced the number of sites with sufficient data to 111.

Correlations are either Pearson r or Spearman r_s, the former used where frequency distributions are known to approximate a normal distribution. Sites were compared using the General Regression Module (Main effects ANOVA, forwards stepwise entry) and principal components analysis (PCA) in STATISTICA 64 version 9.1 (Statsoft Inc., Tulsa, OK, USA). Each flight period variable was entered against site and year of transect record (forwards stepwise solution). A post-hoc Newman-Keuls test was applied to determine the homogeneity of site data for the Great Orme with other sites. All variables were tested for normality of frequency distributions. For the PCA, sites were examined in a reduced space for flight period mean (wWKmean), flight period range (wWKcv), flight period earliest week (WEEKmin), flight period last week (WEEKmax), and flight period range (WEEKrange); grid east and grid north were entered as supplementary variables.

The UKBMS data do not necessarily cover the same period of years, which may well affect summary measures of flight period. Moreover, later years may display features related to climatic change. Consecutive data for the Great Orme cover the period from 1999 to 2012. Subsequently, for more stringent tests of the position of the Great Orme for flight data, we compared UKBMS sites which have at least 10 years of data post-dating 1998 (41 sites).

Results

Wing expanse and wing spot size

Wing spot size was found to correlate significantly with wing expanse (Pearson r = 0.89, P < 0.0001; see Dennis 1977; Dapporto et al. 2019). Sites differed significantly for wing expanse (males: $F_{14,466} = 33.7$, P < 0.0001; females $F_{14,344} = 38.3$; P < 0.0001). In both sexes, a Bonferroni *post hoc* test revealed that the Great Orme samples were smallest in wing expanse and differed from those of all other populations tested (P < 0.0001). At the other extreme (populations with the largest wing expanse) three sand dune populations were homogenous (Prestatyn Sands, Aberffraw and Morfa Harlech; P > 0.18); the remaining populations formed a single residual homogeneous unit.

Wing expanse of the Great Orme population increased over the flight period (days) (Spearman r_s: males 0.39, n = 72, P < 0.001; females 0.25, n = 58, P = 0.06). The correlation for females is not quite significant, perhaps owing to the samples concentrating in the earlier part of the female flight period; when divided about a break in the frequency distribution for days (40 days from June 1), the later butterflies were found to be significantly larger than the earlier butterflies ($t_{56} = 2.18$, n = 35 and 13; P < 0.05). Differences in cohorts of emerging butterflies may occur within the first month of emergences; for instance, males differ for wing expanse when divided about the mode of the sampled individuals (day 25) ($t_{70} = 2.84$, n = 28, 44; P < 0.01).

Flight period

Sites also differ significantly for mean flight period (WEEKmean, $F_{110,1322} = 9.80$, $P < 0.0001$; wWKmean, $F_{110,1322} = 11.20$, $P < 0.0001$). The Great Orme falls into the group of sites having the lowest means (on par with the Orme), including 25 and 22 sites respectively.

Sites also differ for all other flight season variables. Using the entire dataset including all sites with a minimum of 5 years of complete runs of data through the flight period, sites differ significantly for the first appearance of the flight season (WEEKmin, $F_{110,1322} = 9.60$, $P < 0.0001$). A *post hoc* homogeneity test revealed the Great Orme to be unique, distinct from all other sites, and having the earliest flight date (WEEKmin, 10.07). Apart from the Great Orme, sites with the earliest flight dates are those on the Lancashire Morecambe Bay limestones (Arnside 12.31) and on Alderney in the Channel Islands (Trois Vaux 12.80), two to three weeks later (Fig. 3). Early emerging individuals are expected to occur and have been reported at a number of other sites (e.g., Pitts Wood Inclosure in the New Forest, Hampshire), but these are unusually early for those sites and result in an aberrant (very high, implicating negative values) coefficient of variation in flight period.

Sites differ for final week of the flight period (WEEKmax, $F_{110,1132} = 10.1$, $P < 0.0001$) and for measures of variation (WEEKrange, $F_{110,1132} = 10.68$, $P < 0.0001$; WEEKcv, $F_{110,1132} = 6.11$, $P < 0.0001$; wWKcv, $F_{110,1132} = 3.00$, $P < 0.0001$). For the final week of the flight period, the Great Orme belongs to a group of 20 sites with late flight periods. For measures of coefficient of variation, it is unique in having the widest span of flight periods for the unweighted measure (WEEKcv; Fig. 4) and it belongs to a small group of just three sites for the weighted measure (wWKcv), the other two located in Morecambe Bay.

A more stringent test of relationships is attained by restricting analysis (ANOVA) to sites with 10 or more years of data post 1998. Very similar results were obtained (WEEKmean, $F_{40,468} = 15.24$; wWKmean, $F_{40,468} = 20.42$; WEEKmin, $F_{40,468} = 12.7$; WEEKmax, $F_{40,468} = 13.46$; WEEKrange, $F_{40,468} = 12.47$; WEEKcv, $F_{40,468} = 8.00$; wWKcv, $F_{40,468} = 3.35$; all $P < 0.0001$). In these analyses, the Great Orme was unique in *post hoc* Newman-Keuls tests (single group member of an extreme condition) in having the earliest flight period and the longest flight period (wWKcv, WEEKcv and WEEKrange). For mean flight period it was in the group with earliest flight periods (5^{th} of 11 sites for WEEKmean; 2^{nd} of 7 sites for wWKmean) and in the group for the latest flight period (7^{th} of 10 sites).

When sites with data for 5 or more years (n = 111) are examined there is a low correlation between number of years of data and final week of flight period and length of flight period (WEEKmax, Spearman r_s = 0.22, P = 0.02; WEEKrange, r_s = 0.26, P = 0.01), but not with first week (WEEKmin), mean flight period week (WEEKmean) or the alternative measure of length of flight period (wWKcv) (P > 0.43). There is no significant correlation for any of the flight period variables with numbers of years of data when only sites with 10 or more years of data are included (n = 64, r_s, P = 0.06 to 0.72).

Relationship of flight period variables with geography

Flight period is affected by geography; relationships were sought first using sites from all periods with 5 years of suitable data. There is no relationship of extent of flight period (wWKcv, WEEKrange) with grid north or east. Mean flight period (wWKmean) is earlier further north (r = -0.31, P = 0.001) and to the west (r = 0.33, P < 0.001) of the British Isles. So, too, is the final date for flight period (WEEKmax with north, r = -0.26, P < 0.01; WEEKmax with east, r = 0.25, P < 0.01). The earliest date for flight period is similarly affected but to a lesser extent (WEEKmin with north, r = -0.19, P = 0.05 [Spearman r_s = -0.23, P < 0.05]; WEEKmin with east, r = 0.22, P < 0.05). In a multiple regression (stepwise entry) of earliest flight time (WEEKmin) with both grid east and grid north, only east was significant ($F_{1,109}$ = 5.65, P < 0.05) and the Great Orme is a distinct outlier from the regression line (standardised residual = -3.77). In similar regressions for mean flight period (wWKmean) and latest flight period date (WEEKmax), both north and east proved to be significant predictors (wWKmean, $F_{2,108}$ = 10.70, P < 0.0001; WEEKmax, $F_{2,108}$ = 6.36; P < 0.05); in neither case was the Great Orme an outlier. Grid east correlates with grid north for sites (r = -0.22, P < 0.05).

Relationships were then tested using sites with 10 or more years of data for the period post 1998. All flight period variables, except length of flight period (WEEKcv, wWKcv, WEEKrange, P > 0.32), are correlated significantly with geography (grid north and grid east). Mean flight period becomes earlier in the north (WEEKmean, r = -0.44, P < 0.01; wWKmean, r = -0.46, P < 0.01) and west of Britain (WEEKmean, r = 0.45, P < 0.01; wWKmean, r = 0.43, P < 0.01). First week of the flight period is earlier further north (WEEKmin with north, r = -0.34, P < 0.05) and tends to be earlier further west (WEEKmin with east, r = 0.26, P = 0.09). Maximum date (final week) of flight period increases eastwards (WEEKmax with north, r = 0.43, P < 0.01) and tends to decrease northwards (WEEKmax with north, r = -0.30, P = 0.05). A regression analysis (stepwise entry) of earliest flight period against grid north and grid east produced a significant relationship for grid north only

($F_{1,39}$ = 5.04, P < 0.05); the Great Orme is an outlier from the regression line. In a regression analysis for mean flight period, both grid north and grid east are significant ($F_{2,38}$ = 9.98, P < 0.001; there are no outliers); regressions for all length of flight period variables failed. Morecambe Bay sites tend to form a string of negative residuals from the regression line, as illustrated for mean flight period when regressed against grid north and grid east (Fig. 5).

Overall relationship of sites to flight period variables

The position of the Great Orme, and other sites for *H. semele*, in relation to flight period variables and geography is illustrated in a principal components analysis for all sites with five or more years of data, in which flight variables are treated as active variables and grid north and grid east as supplementary to the analysis (Fig. 6). The first two vectors returned eigenvalues > 1 (axis 1, 54.4% of variance; axis 2, 39.0% of variance), accounting for 93.4% of the variance, and distinguish the first week of the flight period and length of flight period (WEEKmin, wWKcv, WEEKrange) from mean flight period timing and the last week of the flight period (wWKmean, WEEKmax) (Table 2). Sites from different regions tend to cluster. However, the Great Orme is a distinct outlier from the cloud of points for the remaining British sites.

Distribution and abundance on the Orme

The grayling butterfly is not abundant over the entirety of the Great Orme but is concentrated on the scars, screes and short steep grass slopes on the southern and western sides in seven 1km squares (Fig. 7). Occasionally the population can become very large as in 2005 and 2010, providing large numbers of potential migrants for surrounding locations. However, from years which return low UKBMS counts, it is clear that the butterfly is not always abundant on the Great Orme.

Discussion

The present study confirms the distinctive characteristics of the Great Orme population of *H. semele* (Thompson 1944; Dennis 1977), especially the highly unusual wing features (small size of wings and wing ocelli) and flight period characteristics (early emergence) of the population. The Great Orme population is also distinct in wing spot characteristics when these are standardised on wing expanse (Dapporto et al. 2019). The present study also demonstrates that the population is highly unusual, perhaps unique, among those currently included in the UKBMS by consistently having the earliest flight period and greatest length of flight period throughout Great Britain, Northern Ireland, the Isle of Man and the Channel Islands. Corresponding with the long flight period is evidence that phenotypic characteristics change through the flight season; wing expanse increases significantly during the latter part of the flight period.

The immediate question is: are these adaptations expected for a coastal site in this westerly and northerly position, bearing in mind the observations arising from work by Roy and Asher (2003) and Roy et al. (2015)? The evidence is that they are. Clearly, the factors involved extend beyond simply the substrate (Carboniferous limestone) as the populations found south of the Great Orme and in the vicinity of Morecambe Bay, although displaying features approaching those found in the Great Orme population, are nothing like so extreme. In fact, the reasons for this unusual population have long been considered by RLHD to be founded in the unique and extreme characteristics of the local climate (high radiation levels, mild winters, excessive wind speeds, desiccated host plants) of the Orme's Head, and its joint effect both on larval feeding times and rates and the capacity of adults to fly (see Maclean et al. 2017). These factors have now been explicitly modelled in Dennis and Hardy (2018, Appendix 15). It is considered that the Great Orme population being so large may well have persisted since arrival in the early Holocene and evolved its unusual characteristics during the mid-Holocene period of higher temperatures. If this is the case, then higher temperatures projected for climatic change (Settele et al. 2009) should not pose a threat, especially as there are slopes contrasting markedly in slope angle, aspect and cover that the butterfly can occupy on the Great Orme.

Even so, the characteristics of the Orme population may be even more unusual than so far disclosed. It is likely that both the length of the flight period and the significance of changes in phenotype of Great Orme *H. semele* are underestimated in this study. First, sampling of individuals for assessing phenotype has been biased to the earlier part (from the third week of June), but not the earliest part, of the flight period (Dennis 1977). Secondly, the position of the UKBMS transect on the Great Orme (largely covering SH 7682, SH 7782 and the southernmost part of SH 7683; see Fig. 5), though taking in the full elevation from sea level to the summit, is restricted to the southern and south-western aspects; south-eastern, western and north-western slopes are not surveyed, nor are the relatively level areas of mine waste at Mynydd Isaf (SH 776831) or the limestone pavements at the distal end of the peninsula (SH 756838), which the species also occupies later in the season (Dennis and Bardell 1996). Thus, later cohorts of individuals on the Great Orme may be missed by the current transect. The implication is that the Great Orme population is unique among those found on British mainland for early emergence, length of flight period and wing phenotypes (especially wing size and wing ocelli) (Dapporto et al. 2019).

The distinctions in wing phenotype for the Great Orme population are long known to have a genetic basis (Dennis 1977); the wing and flight period transformations have been modelled on contemporary site factors (Dennis 1977, 1992; see Dennis and Hardy 2018, Appendix 15). A key feature is the demonstration that individuals from the sand dune populations of the butterfly elsewhere in North Wales (Prestatyn; Aberffraw, Harlech) are much larger than those found on limestones or other substrates (Dennis 1977). However, the size (wing expanse) of individuals in populations on the sand dunes adjacent to the Great Orme, on Llandudno Sands (SH 7781) and Conwy Morfa (SH 7779), is much less than that of individuals on sand dunes elsewhere; in fact the reduction in size of individuals from Llandudno Sands and Conwy Morfa is similar to that of the Great Orme population when it, in turn, is compared with populations on nearby limestone slopes of the Creuddyn Peninsula (i.e., SH 7981, 7980), to which the Orme belongs, south of Llandudno (Dennis 1977). Moreover, it has been suggested that the increase in size of individuals throughout the extended flight period may well conceal the presence of a later emerging distinct population on the Great Orme (Dennis 1977), arising from migrants that were (or still are) able to occupy the headland once the vegetation was opened up outside the sparsely clad scars and screes following human settlement by farming and mining activity (since the Neolithic) (Bannerman and Bannerman 2001). The genetic integrity of the early and later emerging individuals could well be maintained by ecological differences leading to temporal isolation (Dennis 1971; see Boumans et al. 2017).

The knowledge that there has been exchange of individuals between the Great Orme and adjacent populations is of long standing (Dennis 1977). The current study, in conjunction with improved knowledge of the ability of all butterflies to transfer to offshore islands, many isolated from the mainland (Dennis et al. 1998; Dennis and Hardy 2018), raises the prospect that more distant locations have been influenced by movements of individuals from the Great Orme (see Dapporto et al. 2019). Bearing in mind that the Orme population can at times be very large, this outcome should not be discounted (Tilley and Dennis 2017). The populations of *H. semele* from the Morecambe Bay area also feature tendencies to early emergences, long flight periods and small individuals (Dennis, unpublished data); this is most evident in the residual string of Morecambe Bay sites when flight characteristics (i.e, first appearance, mean flight period, length of flight period) are related to grid north (Fig. 5). A further point of importance is that the sites in Morecambe Bay and surrounds (Whitbarrow Scar; Hutton Roof, Holme Fell) are on the same substrate as the Great Orme (Carboniferous limestone) and share many of the same topographic and substrate attributes of the Orme. But, then, populations found on other outcrops of Carboniferous limestone on the Creuddyn Peninsula immediately south of the Orme and Llandudno differ substantially from the Great Orme population in wing features and phenology (Dennis 1977). The Great Orme is unusual from other sites in being highly exposed to strong prevailing winds, salt spray and high radiation levels (Dennis and Hardy 2018).

In time, with developing techniques in molecular biology, it will become possible to track down the precise genetic distinctions in the Orme population of *H. semele*. When this butterfly is thoroughly studied, it would be a valuable exercise to examine the relationship of *H. semele* populations around Morecambe Bay and the Isle of Man to that on the Great Orme and Creuddyn Peninsula. An interesting aspect of the flight period that fits a contemporary ecological model for the Orme population (Dennis and Hardy 2018) is the observation made in this paper of earlier flight periods in the north and west of Britain (Roy and Asher 2003), a feature that coincides with smaller individuals northwards in Britain (Dennis, unpublished data). Smaller individuals tend to have shorter development times which could facilitate earlier emergences. This is likely to be linked to the grayling's distinctive coastal distribution over much of Britain and overwintering larvae being able to start feeding earlier in the higher minimum temperatures of coastal environments (see Dennis 1992).

Conclusions

The present study supports the notion of a unique population of *H. semele* on Great Orme's Head, a uniqueness that we suggest extends to genome composition; in this sense it conforms to an 'evolutionary significant unit' (ESU) (Casacci et al. 2014). Moreover, there are indications in this population of sympatric evolutionary development, providing valuable insights into incipient speciation. Such populations are irreplaceable as genetic reserves and deserve special attention; research to disclose genome uniqueness and resource dependency to facilitate long-term management. The headland has now become a priority for conservation as it is a hot spot for butterfly species in Northern Britain, a key site for rare plants and animals and with outstanding geological and archaeological features. Flagship species provide a focus for conservation efforts (Simberloff 1998; Thomas-Walters and Raihani 2017). *H. semele* and *Plebejus argus* are flagship species for the butterfly fauna on the Great Orme (Dennis and Hardy 2018). The population of Great Orme's Head *H. semele* is accompanied by other unique (e.g., Great Orme Berry, *Cotoneaster cambricus*; Dickoré and Kasperek 2010) or rare (e.g., Silky Wave, *Idaea dilutaria*; Anon 2016 and Horehound Plume-moth, *Wheeleria spilodactylus;* Menéndez and Thomas 2000) components. We advocate the need for a detailed study of the grayling butterfly on this headland and surrounding coastal locations for this butterfly, especially as the species is undergoing serious national decline as mentioned earlier (Fox et al. 2015).

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Compliance with ethical standards

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Tables

Table 1 Sample locations for *Hipparchia semele* in Wales and adjoining parts of England for the measurements of wing expanse and ocelli between 1968 and 1973

Location	OS grid reference	Substrate	Biotope	Males	Females	Total
Great Orme	SH 76481 82868	Limestone	Grassland/scree grazed	72	58	130
Creuddyn Lst[1]	SH 79876 80839	Limestone	Grassland/scree grazed	46	28	74
Conway Morfa	SH 77254 79219	Sand dune	Marram grass, dune	31	21	52
Llandudno Sands	SH 77347 81141	Sand dune	Marram grass, dune	13	5	18
Conwy Mt	SH 75984 77882	Volcanic	Grass/heath, grazed	17	15	32
Allt Wen	SH 74639 77160	Volcanic	Grass/heath, grazed	59	30	89
Aber Valley	SH 69919 73794	Shale	Grassland/scree grazed	29	51	80
Aberffraw	SH 35738 68257	Sand dune	Marram grass, dune	52	37	89
Morfa Harlech	SH 56987 31761	Sand dune	Marram grass, dune	14	15	29
Bwrdd Arthur	SH 58415 81416	Limestone	Grassland/scree grazed	24	7	31
Trearddur Bay	SH 25407 78633	Metamorphic schist	Grass/heath, grazed	12	6	18

Rhyd y Foel	SH 91404 77660	Limestone	Grassland/scree grazed	32	15	47
Moel Hiraddog	SJ 06303 78156	Limestone	Grassland/scree grazed	34	27	61
Warren, Prestatyn	SJ 09589 84438	Sand dune	Marram grass, dune	36	34	70
Marford Quarry	SJ 35669 55997	Fluvio-glacial outwash	Grassland/broom scrub; quarry	10	10	20

[1] Samples from two locations on Creuddyn Peninsula south of Llandudno town; reference given for largest sample

Table 2 Component loadings (correlations between original variables and components) for a principal components analysis of flight period variables for *Hipparchia semele* (sites used have 5 or more years of suitable UKBMS data). Communalities give cumulative explained variance for axes, in this case the first two axes. High loadings (>50% variance) are marked in bold font

Active variables	Axis 1	Axis 2	Communalities
Flight period mean (wWKmean)	0.53	**-0.83**	0.97
Flight period range (wWKcv)	**-0.89**	-0.04	0.79
Flight period earliest week (WEEKmin)	**0.94**	-0.29	0.96
Flight period last week (WEEKmax)	-0.26	**-0.96**	0.99
Flight period range (WEEKrange)	**-0.84**	-0.51	0.96
Supplementary variables			
Grid east	0.12	-0.30	0.11
Grid north	-0.07	0.30	0.09

Figures

Fig. 1 The distribution of sample sites for wing morphology data collected in North Wales between 1968 and 1973. Sites: black, limestone; white, sand dunes; grey stipple, other geology (igneous, metamorphic and other sediments).

Fig. 2 Distribution of UKBMS sites used for determining flight period characteristics in *Hipparchia semele* over the UK mainland (open symbols, sites with 5 or more years of data (n=111); closed symbols, sites with 10 or more years of data postdating 1998 (n=41)). Owing to the overlap of sites not all are evident on the map.

Fig. 3 Box plot of flight period (first week; mean ± 2 standard errors) of *Hipparchia semele* over sites with suitable records (> 5 years of data; see text). Names of sites on the X axis have been ordered from south (left) to north (right) and only each second location labelled to assist clarity.

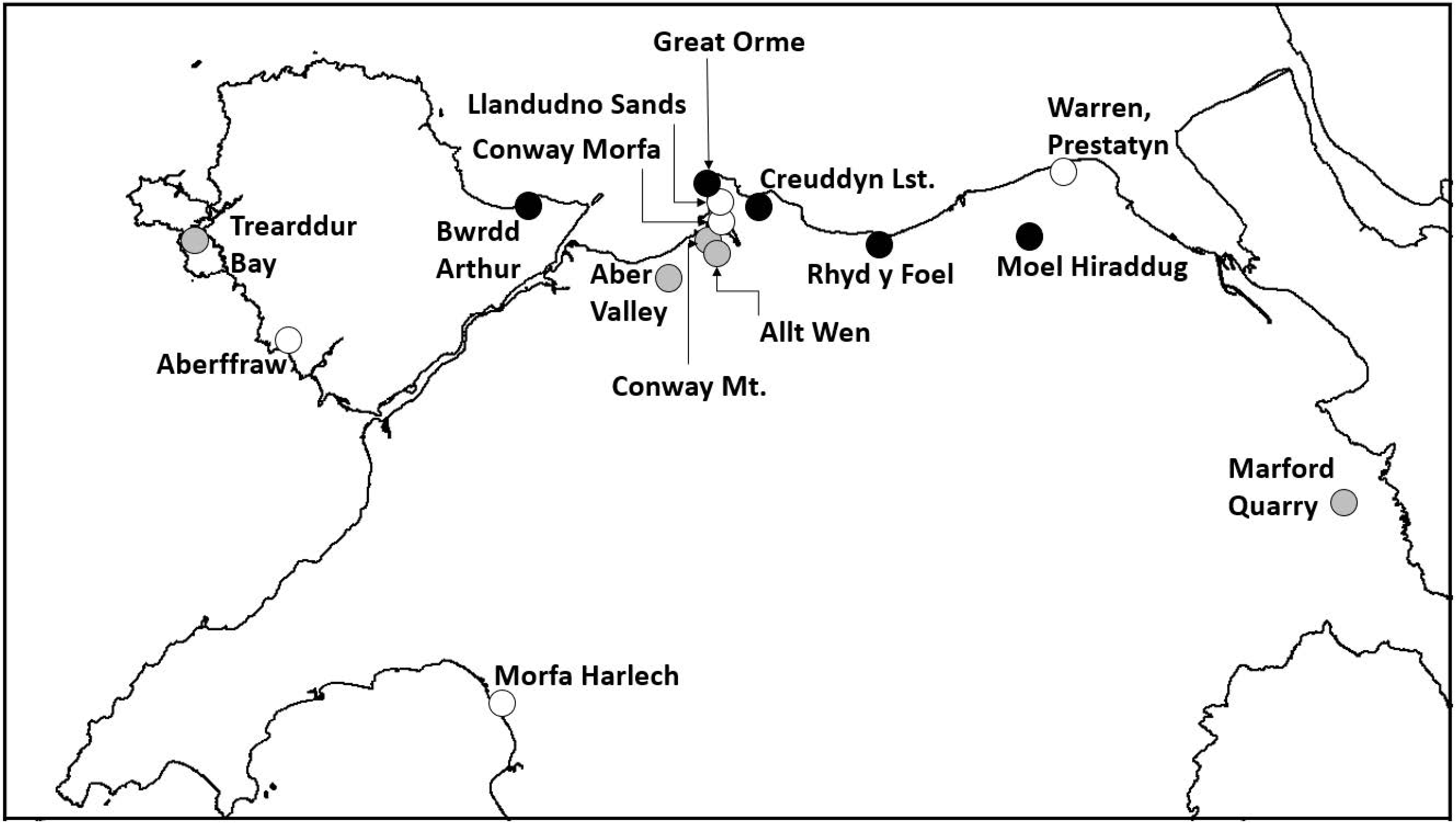
Fig. 4 Box plot of flight period (coefficient of variation; (mean ± 2 standard errors) of *Hipparchia semele* over sites with suitable records (over 5 years of data; see text). Names of sites on the X axis have been ordered from south (left) to north (right) and only each second location labelled to assist clarity.

Fig. 5 The relationship of flight period (mean flight period, WEEKmean) with grid north and grid east for sites having 10 or more years of data post-dating 1998 ($F_{2,38} = 9.98$, $P < 0.001$, grid north beta -0.40, grid east beta 0.37; $R^2 = 34.3\%$). Observed versus predicted dates shown. The string of marked dots (largely negative residuals) in the middle of the graph includes sites from the Carboniferous limestone around Morecambe Bay, Lancashire (blue: open circles, at the coast; closed, >5km inland); blue square, Great Orme.

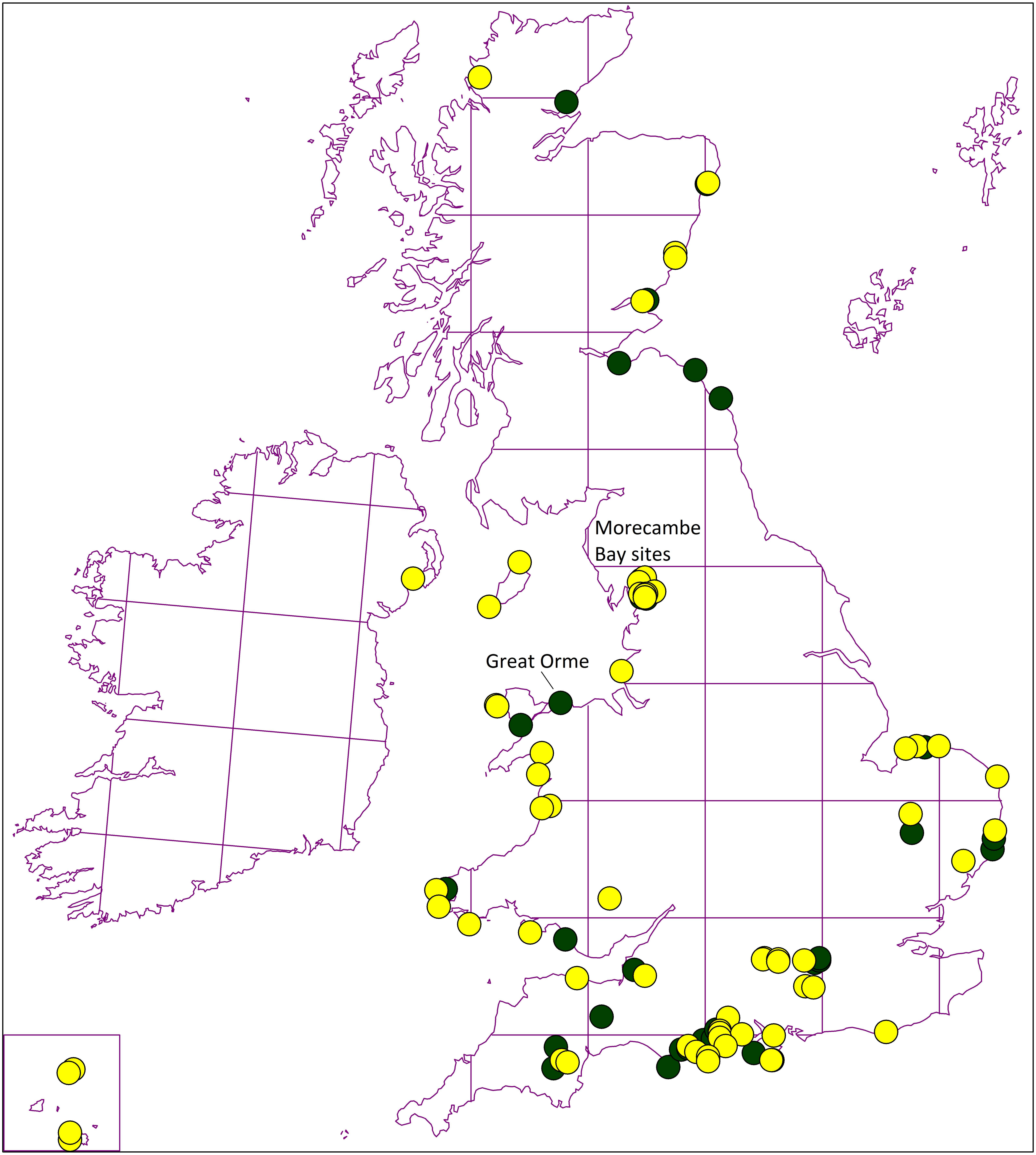
Fig. 6 Principal components plot of flight period characteristics of grayling populations with > 5 years of records. Axis 1, 54.4% of variance; axis 2, 39.0% of variance. The Great Orme is an outlier on Axis 1 which accounts for earliest flight period date and length of flight period (see Table 2). Morecambe surrounds include more inland sites on the Carboniferous limestone to the north at Whitbarrow Scar (SD 4587) and to the east Hutton Roof (SD 5479).

Fig. 7 Distribution of *Hipparchia semele* on the Great Orme's Head during 1995 and 1996. 1km grid squares shown. (Modified from Dennis and Bardell 1996).

Hipparchia semele sites

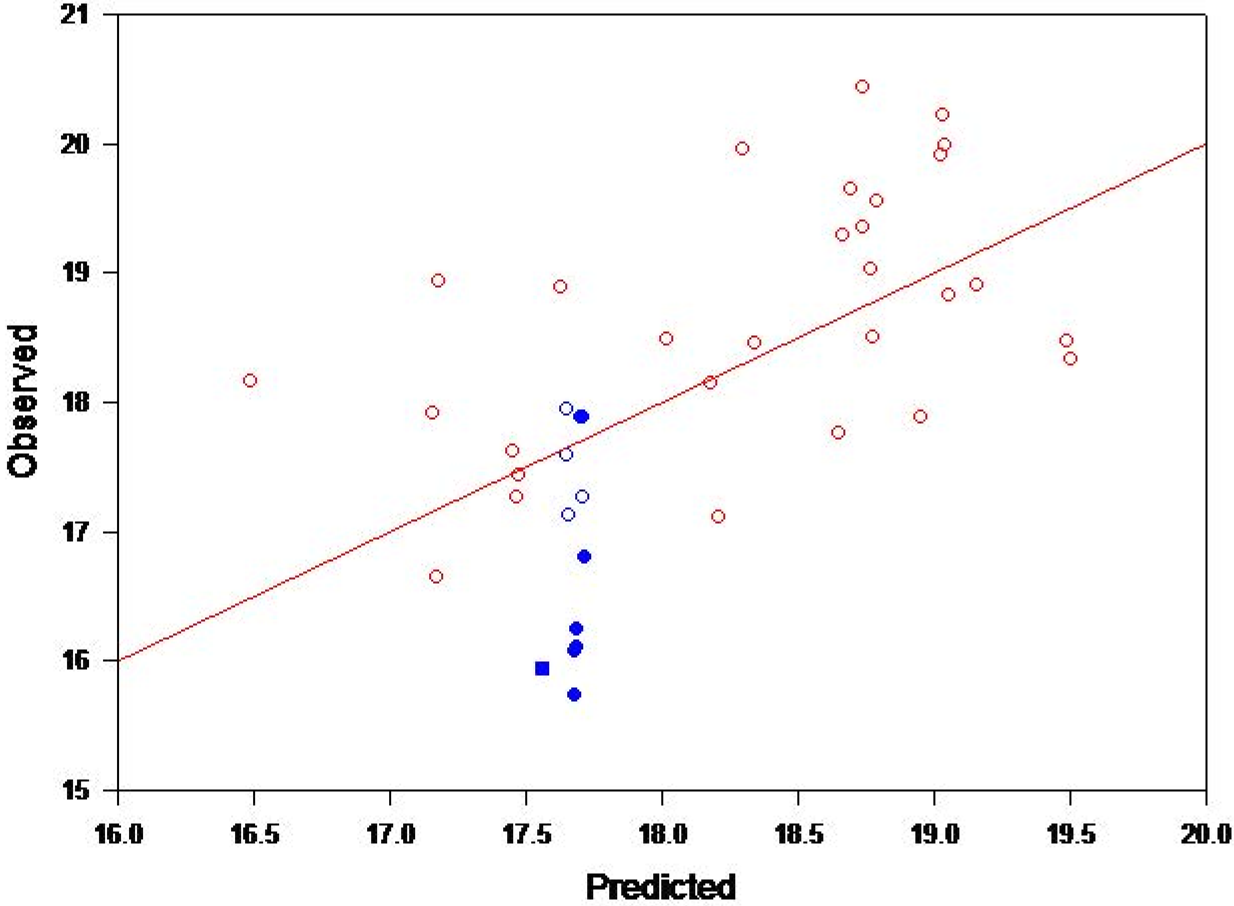


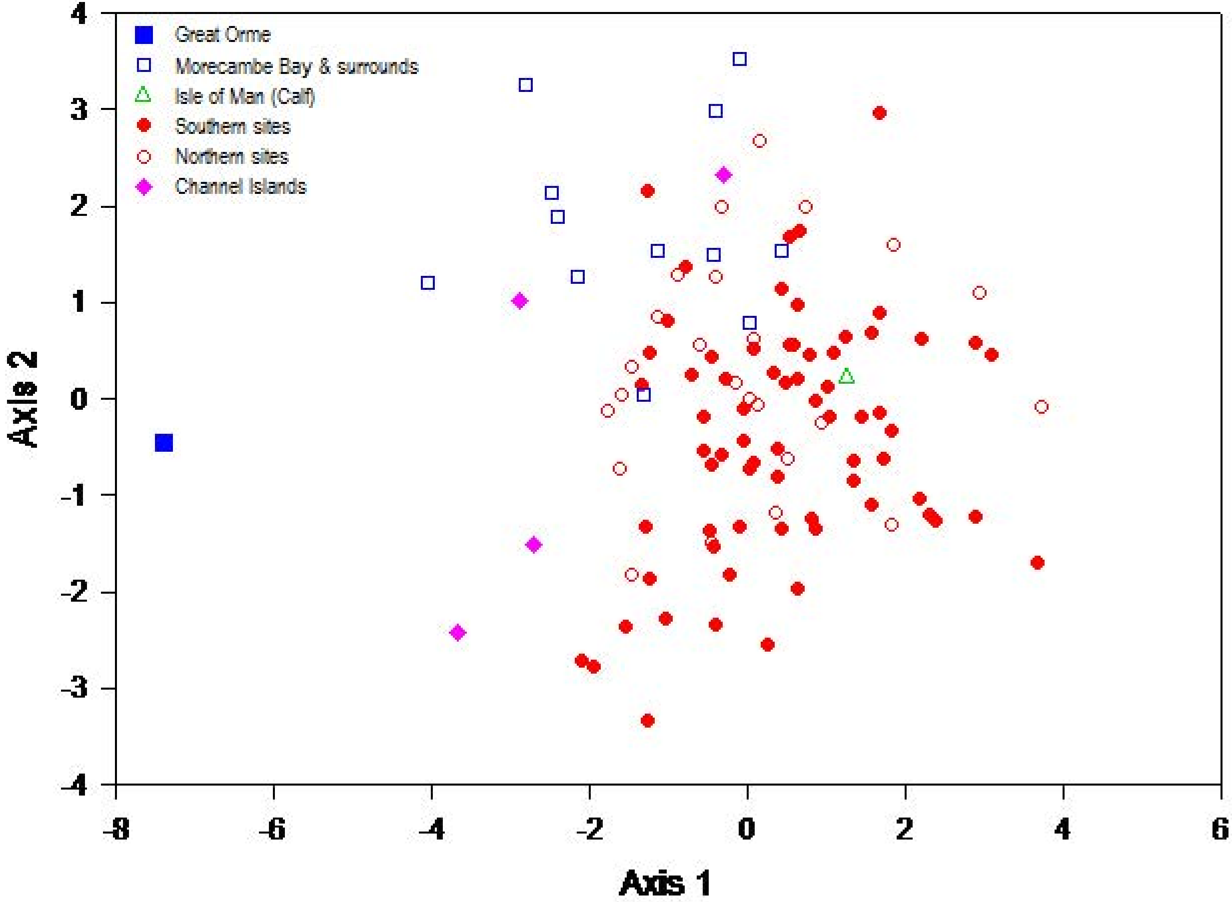
Hipparchia semele



Mean
Mean ± 2*SE
Flight week (earliest)
22
20
18
16
14
12
10
8
Great Orme
Location
Les Blanches Banques
Trois Vaux
Aish Tor
Bovey Heath
Durlston CP East
Ventnor
Studland Heath
Mottistone Down
Tadnoll
Piddledown Common
Hengistbury Head
Upton Heath North
Sopley Common
The Commons Roydon
Lullington Heath
Avon Heath CP North
Pitts Wood
Witley Common
Bossington
Crook Peak
Silchester Common
Chobham Common
Greenham Common
Chobham Common NE
Oxwich
Skomer
Ramsey Island
Malvern
North Warren
Dunwich Forest
Walberswick
Dyfi
Winterton Dunes
Coedydd Maentwrog
Holkham
Scolt Head Island
South Stack Ranges
Great Orme
Calf of Man
Warton Crag RSPB
Leighton Moss
Arnside Knott NT
Heathwaite NT
Gait Barrows NNR
Burton Fell
Holme Park Fell
Witherslack Woods
Whitbarrow NNR
Helsington Barrows NT
Lindisfarne
Salisbury Crags
Tentsmuir Point
Tentsmuir Point North
St Cyrus
Sands of Forvie
Pollymore

Mean
Mean ± 2*SE
Great Orme
Flight week (coefficient of variation)
Location
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
Les Blanches Banques
Trois Vaux
Aish Tor
Bovey Heath
Durlston CP East
Ventnor
Studland Heath
Mottistone Down
Tadnoll
Piddledown Common
Hengistbury Head
Upton Heath North
Sopley Common
The Commons Roydon
Lullington Heath
Avon Heath CP North
Pitts Wood
Witley Common
Bossington
Crook Peak
Silchester Common
Chobham Common
Greenham Common
Chobham Common NE
Oxwich
Skomer
Ramsey Island
Malvern
North Warren
Dunwich Forest
Walberswick
Dyfi
Winterton Dunes
Coedydd Maentwrog
Holkham
Scolt Head Island
South Stack Ranges
Great Orme
Calf of Man
Warton Crag RSPB
Leighton Moss
Arnside Knott NT
Heathwaite NT
Gait Barrows NNR
Burton Fell
Holme Park Fell
Witherslack Woods
Whitbarrow NNR
Helsington Barrows NT
Lindisfarne
Salisbury Crags
Tentsmuir Point
Tentsmuir Point North
St Cyrus
Sands of Forvie
Pollymore


21
20
19
18
17
16
15
Observed
16.0
16.5
17.0
17.5
18.0
18.5
19.0
19.5
20.0
Predicted


Great Orme
Morecambe Bay & surrounds
Isle of Man (Calf)
Southern sites
Northern sites
Channel Islands
Axis 2
Axis 1
4
3
2
1
0
-1
-2
-3
-4
-8
-6
-4
-2
0
2
4
6

Hipparchia semele