

Resource requirements, behaviour, and weather constraints on activity of the butterfly *Aporia crataegi* in Normandy, France

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Abstract

The Black-veined white butterfly (*Aporia crataegi*) is a widespread Palearctic species facing substantial declines across its European range. This species became extinct in the British Isles in the 1920s. However, the projected drying climate in south-eastern Britain could provide suitable conditions for a reintroduction attempt.

The aim of this study is to identify the resource requirements of adult *A. crataegi*, including egg-laying, feeding, roosting, and mating, and to collate information on individual longevity and mobility. We also investigate how environmental resources and weather affect adult activity. We found that *A. crataegi* used a variety of nectar resources but had a distinct preference for the flower colour purple. Females laid eggs mainly on small plants of *Prunus spinosa* and *Crataegus monogyna* and significantly preferred isolated host plants or those in defunct and gappy hedgerows. *Aporia crataegi* was positively associated with the percentage of host and nectar plants and showed a positive relationship with a heterogeneous distribution of host resources, a homogeneous distribution of nectar resources, and much spatial overlap of these resources. Air temperature, solar radiation intensity, and windspeed affected the activity of both sexes. Under cloudy conditions, sexes were active at different temperatures with females needing higher temperatures and solar radiation than males to become active.

Implications for insect conservation Our results provide fine-scale microhabitat and climatic requirements of *A. crataegi* including oviposition sites, resource composition, organisation and distribution requirements, which are key to supporting evidence-based conservation strategies within this species current range, as well as in support of a reintroduction attempt.

Introduction

Insects are a vital component of global biodiversity, with a crucial role in the functioning of ecosystems (Schowalter et al. 2018). However, wild terrestrial insects are undergoing severe global declines (Potts et al. 2016; Seibold et al. 2019) with the potential of ecosystem collapse (Wagner 2019; Cardoso et al. 2020; Rumschlag et al. 2023). In the western Palaearctic, monitoring indicates that such declines are severe amongst Lepidoptera, with evidence for regional losses of specialised species which require a limited range of resources accompanied by declines of general species abundance using a wider range of resources (Thomas 2016; Warren et al. 2021a). Habitat loss and landscape degradation, isolation, and fragmentation, and more recently climate change, are widely recognised as main drivers of Lepidoptera decline (Warren et al. 2021b), and the consequence of differential rates of declines is regional homogenisation as specialist species are lost (Dapporto et al. 2015). Conservation strategies to mitigate and prevent losses, including re-introductions at local, regional, and national levels, can be effective, particularly if species resource requirements are known and can be maintained within landscapes. However, resource requirements can be complex, comprising consumables (e.g., hostplants, resting and roosting sites, feeding resources, mating sites, refuges from predators) and utilities (thermal regimes and specific climate) and need to include those required by all life-history stages (Dennis et al. 2003).

Thus, hostplants and broad vegetation descriptors are not precise predictors of presence or abundance (Dennis et al. 2003).

The Black-veined White butterfly (BVW, *Aporia crataegi*) is treated as a common, widespread Palearctic species, although it has undergone substantial declines across its European range (Asher et al. 2001). It is considered Critically Endangered in Austria (Koschuh and Gepp 2004), and it has suffered local extinctions in the Netherlands and Czech Republic. In the British Isles it is described as persisting until 1927 in southern and central Britain, with local extinctions recorded in different year, e.g. extinction in Devon dating 1862 (Bristow 1993), but the precise cause of its extinction is unclear, although it has been attributed to the spread of fungal disease in larval stages due to high summer rainfalls (Pratt 1983). Currently, the Black-veined White butterfly range margins are changing, with a described northern expansion in Finland and Denmark (Asher et al. 2001) and an upward elevation shift in southern mainland European (Merrill et al. 2008), possibly indicative of responses to climate change (Carroll et al. 2009) and habitat change.

Bioclimatic models revealed that the projected drying climate in south-eastern Britain is expected to provide conditions that are highly suitable for this butterfly, at least until 2050 (Carroll et al. 2009). For these reasons, the BVW has recently been identified as a suitable candidate for a reintroduction attempt to the south of England (Thomas et al. 2025). Previous known attempts at re-introduction have failed, likely due to the number of individuals and the scale of release being too small (Thomas et al. 2025), as well the inappropriate habitat conditions at the release sites (Oates and Warren 1990). Some evidence is available on the nectar and hostplant preferences of *A. crataegi* (Merrill et al. 2008; Jugovic et al. 2017b; Jugovic and Kržič 2019), though the precise microhabitat of hostplants used by this species, and the weather constraints on adult activity are not well documented. Addressing these questions will inform effective conservation practices within the existing range of this species and support the development of an evidence-based reintroduction programme in southern England.

This study aims to address the following objectives during three seasons (2008,2009, 2024) in Normandy, northern France: (1) identify the resource requirements of adult *A. crataegi*, including those required for egg-laying, feeding, roosting, and mating; (2) provide information on the habitat and vegetation structures used by the species and how its abundance is influenced by resources, together with information on individual longevity and mobility; (3) determine the effects of weather on adult activity.

Research methods

Study species

Aporia crataegi is a widespread Palearctic species, distributed from Western Europe and North Africa to Asia between 40–70°N, including Japan (Tolman and Lewington 2008). In Europe, this species is described as occupying dry grassland, shrubland, and woodland edges (Jugovic et al. 2017a), where nectar plants and larval hostplants such as *Prunus* spp. and *Crataegus* spp. occur (Asher et al. 2001).

Eggs are laid mainly in July in batches of 100–200, generally on the upper surface of leaves of host plants. The larvae shelter in groups feeding on the leaves of the hostplant during summer and overwintering in silky webs. In spring, they continue feeding in a group but abandon the gregarious lifestyle and disperse before pupating (Merrill et al. 2008). Depending on location and weather conditions, the flight period of *A. crataegi* lasts from April to July (Tolman and Lewington 2008).

Study sites

Studies were conducted over three seasons (June 11–27, 2008, June 18–July 3, 2009, and June 06–26, 2024) in three locations of Normandy, France, characterised by broadly different habitat types (Fig. 1a). The 2008 and 2024 study sites consisted of wet meadows, grasslands and private gardens located in Orne, Basse Normandy (Fig. 1b,d), some surrounded by species-rich hedgerows embedded in an agricultural and urban matrix. The 2009 study sites consisted of three dry, herb-rich neutral grassland patches, with elements of calcareous grassland and ruderal agricultural weed communities surrounded by an area of intensive cereal production in Calvados, North of Normandy (Fig. 1c). Supplementary data from the low Alps is derived from six different locations comprising calcareous and neutral grassland and scrub and woodland matrices at elevations of 250–1850 m AOD as part of a study butterfly resource requirements, conducted between late May and mid-July in 1997, 1999 and 2001.

Adult behaviour and resource use

At the northern French sites (2008–2009), individuals were followed between 08.00 and 18.00 hr, and their behaviours and sexes recorded to gather information on resource use. Individuals were followed for as long as possible and when lost to observation the next encountered individual was followed. Additional information on behaviour was also recorded during mark-release-recapture events at each site (see below). Supplementary data from each of the low Alp sites was recorded at 5-day intervals at each site between 08.00 and 18.00 hr in each year using continuous fixed routes through each site. At all sites, the precise location, substrate type and height of every settled individual and activity was recorded along with sex, together with measures of % cover of grasses, % bare ground, herb species and shrub species and average vegetation height within a 0.25 m radius of the identified butterfly (Table 1a). Data on weather conditions were collected concurrently (at 1-minute intervals) with behavioural observations with a Skye data logger recording wind speed (msec^{-1}) at 1.4 m, solar radiation intensity (Wm^{-2}) and air temperature at 1.2 m and vegetation temperature at 0.05, 0.3 and 1 m heights. Similarly detailed environmental data were collected in the 2001 low French Alps study.

Table 1

List of parameters recorded in the 2008–2009 seasons during a) individual tracking and at oviposition sites of *A. crataegi*, and b) vegetation sampling using 0.25 x 0.25m random quadrats

Parameters	Type	Unit of measure
<i>a)</i>		
<i>Climatic conditions</i>		
Air temperature	continuous	Degree Celsius
Solar radiation	continuous	Watts m ⁻²
Wind speed	continuous	m s ⁻¹
<i>Microhabitat</i>		
Plant identity (if landed on)	categorical	species name
Plant height	continuous	cm
Herb cover	discrete	percentage %
Shrubs and grass cover	discrete	percentage %
Bare ground	Discrete	percentage %
Maximum herbs height (within 0.25m radius)	continuous	cm
<i>Oviposition site</i>		
N of eggs	continuous	number
Height of eggs on host plant	continuous	cm
Hostplant species	categorical	species
Hostplant height	continuous	cm
Hostplant width	continuous	cm
Position of eggs on leaf	categorical	underside/upper side
Leaf size	continuous	mm
Aspect of eggs	categorical	S, SW, SE, N, NW, NE
Heterogeneity of surrounding vegetation	categorical	1 = low, 2 = medium, 3 = high
Position of hostplant within hedgerow	categorical	solid hedgerow/gappy hedgerow/ isolated shrub
<i>b)</i>		

Parameters	Type	Unit of measure
<i>Vegetation characteristics</i>		
Vegetation height	continuous	cm
Nectar sources cover	discrete	percentage %
Grasses cover	discrete	percentage %
Herbs cover	discrete	percentage %

Egg-laying site microhabitat selection

To determine the microhabitat characteristics of egg-laying sites, standardised egg searches were carried out in 2008 and 2009. The first 20 *P. spinosa* and *C. monogyna* encountered on a 3 m strip along and adjacent to the hedgerows bordering those areas where females were active were searched for eggs. Where fewer than 20 plants were encountered, all available host plants were searched (adapted from Merrill et al., 2008). When an egg-laying site was found, we recorded hostplant species, height, spread and the precise location of egg deposition (Table 1a). To compare female choice of hostplant features with their availability on the study sites, a random survey of the used hostplants was performed along the same hedgerows, where the same variables collected during the egg searches were recorded on the first 20 host plants.

Butterfly population size, abundance, and resource characterization

Mark-release-recapture studies were conducted between 10:00 and 16:00 hr along transects to estimate adult abundance and population size at each study site. Transects were walked with temperatures > 13 °C and wind speed less than Beaufort scale 5 (< 29 kmh⁻¹) in June 2008, between the 21st of June and 1st of July 2009, and between the 6th -26th of June 2024. Each butterfly encountered was netted, individually marked using a site-specific colour permanent marker and gently released immediately at the same location. Site specific marks were used to identify any between-site movements in each year. For each individual caught, we recorded sex, behaviour prior to netting, and location within the site. Intervals of 30 min between each walk were maintained to allow the population time to mix and return to normal behaviour levels (Southwood and Henderson, 2000). The data were subsequently analysed using the frequencies of capture method (Craig, 1953). This method was chosen as it has the advantage of giving a population estimate after only one day sampling and is applicable for mobile individuals which rapidly mix with the population after release. For each site in 2008–2009, site vegetation characteristics (height (cm), % cover of nectar sources, % cover of grasses, % cover of herbs) were measured using either 30 or 50 (dependent on-site size and heterogeneity) random 0.25 x 0.25m quadrats (Table 1b).

In 2024, following Turlure et al. (2019), we applied a resource-based habitat approach and computed habitat characteristics using three parameters: (1) resource composition (the diversity of resources) (2) resource availability (the quantity and quality of species-specific resources), and (3) resource

configuration (the organisation and distribution of species-specific resource). Resource composition was assessed using 2m x 2m quadrats positioned using stratified random sampling. Each quadrat was divided in 25 squares (each measuring 40*40 cm) and the number of sample quadrats per site ranged between 16 and 32 depending on site area. We estimated species richness and abundance of each plant, based on their presence in each square (i.e. on a scale of 0 to 25). Data on species-specific ecological resources were extracted from the abovementioned vegetation samples. We measured resource quantity as the abundance of host plant species and nectar plant species averaged across sites. The resource distribution of each host and nectar plant species was computed by quantifying a niche breadth measure (Krebs 2014) using Levin's measure (Levins 1968) equation:

$$B = \frac{1}{\sum p_i^2}$$

where p_i is the proportion of vegetation samples in a site containing the i^{th} abundance level of the host plants or nectar plant species considered. As the number of samples were different among sites, it was standardized before analysis using the formula (Donovan and Welden 2002) below:

$$B_a = \frac{B - 1}{n - 1}$$

where B_A is the standardized niche breadth, n is the total number of samples in the site. After standardization, distribution ranged from 1 (homogeneous distribution; resources are distributed in equal amount) to the degree of heterogeneity of the resource distribution (Turlure et al. 2019).

Resource organization represented the percentage of overlap between host and nectar plant resources and was estimated using Schoener's index (Schoener 1970) of niche overlap equation:

$$O_{la} = 1 - 0.5 \sum |P_{il} - P_{ia}|$$

where p_{il} is the proportion of host resources and p_{ia} is the proportion of nectar resources.

Data analysis

To determine if female butterflies had preferences for particular hostplant characteristics we used Mann-Whitney U tests and Chi square tests. Mann-Whitney U tests were also used to test for sex differences in activity. When full microclimate and durations of activities were recorded, these durations were related to solar radiation, temperature, and wind speed using Linear Models (LM) and independent t-tests.

The effects of vegetation characteristics on the abundance of *A. crataegi* were evaluated using Linear Mixed Effect Models (LMMs) where each vegetation parameter (Table 1b) was fitted as fixed factors and SiteID was used as a random factor.

We used generalized linear models (GLMs) with Poisson distribution to determine the effects of resource availability, composition, and configuration on *A. crataegi*'s population size. We included % host plants, % nectar plant, species richness, distribution of host plants, distribution of nectar plant and organisation as fixed factors. To avoid multicollinearity, two separate models were fitted: Model 1 included the resource composition and availability parameters (i.e., % of host resource, % of nectar resources, species richness), Model 2 included the resource configuration parameters (i.e. distribution and organisation of host and nectar plants) (Table S1, S2). We selected the best models as those with the lowest values of Akaike's Information Criterion (AIC, Burnham and Anderson 2002). Model assumptions were verified by plotting residuals against fitted values and for each covariate in the model. All statistical analyses were conducted in R statistical software version 4.3.2 (2023-10-31) (R Core Team, 2021) with ggcorrplot package (Kassambara, 2019), and car packages (Fox and Weisberg 2019). We used ggplot2 R-package to create the prediction plot figures (Wickham 2016).

Results

Adult behaviour and resource use

Overall, a total of 1 572 individual behavioural observations were made in 2008 and 2009. The most commonly observed behaviours were flying, feeding, basking (settled with wings open), resting (settled with wings closed), courtship and mating, interactions and roosting. Egg-laying flights of females were also recorded. Individuals of *A. crataegi* were found to be mostly active between 9:30 and 18:00 hr, although individuals were recorded up to 20:00 hr during sunny, warm days.

Overall, eleven plant species were used as nectar sources (Table 2). While there were differences between what was used in the study locations, all nectar resources used were blue/purple/red in colour, with most being purple. In cool conditions during the day, and overnight, individuals selected relatively tall plants (0.5-1.5m) in open areas to roost. In all cases these were higher than the average sward height (0.3 to 0.6m). The most commonly used substrates were the undersides of *Leucanthemum vulgare* open flowers (northern France) and the underside of *Apiaceae* umbels in the low Alps (Table 2). No roosting on shrubs or trees was recorded at any location.

Table 2

Resources used by *Aporia crataegi* in Normandy and low Alps of central France. Resources are divided in feeding, egg laying, roosting and resting

Resource type	Site	Species	Height range used
Nectar sources	2008		
	Site 1 & 2	<i>Symphytum uplandicum</i> , <i>Trifolium pratense</i> , <i>Centaurea nigra</i> , <i>Vicia cracca</i>	0.2-1.5m
	2009		
	Site 1, 2 & 3	<i>Cirsium arvense</i> , <i>Melampyrum arvense</i> , <i>Anacamptis pyramidalis</i> , <i>Trifolium pratense</i> and <i>Centaurea nigra</i>	0.1-1.5m
	1997,1999,2001		
	All low Alps sites	<i>Cirsium arvense</i> , <i>Trifolium pratense</i> , <i>Centaurea nigra</i> , <i>Vicia cracca</i> , <i>Vicia sativa</i> , <i>Knautia arvense</i> , <i>Echium vulgare</i> , <i>Ballota nigra</i>	0.1-0.6m
	2024		
Egg laying (host plants)	All sites	<i>Trifolium pratense</i> , <i>Centaurea nigra</i> , <i>Symphytum</i> . Spp., <i>Tuberous Comfrey</i> , <i>Vicia</i> . spp., <i>Leucanthemum vulgare</i> , <i>Ranunculus acris</i>	0.1-1.5m
	2008		0.5-1.5m
	All sites	<i>Prunus spinosa</i> , <i>Crateagus monogyna</i>	
	2009		
Roosting	One site	<i>Prunus spinosa</i>	0.5-1.5m
	2008		
	Site 1 & 2	<i>Oenanthe pimpinelloides</i>	0.5-1m
	2009		
Resting	Site 1, 2 & 3	<i>Leucanthemum vulgare</i> flower undersides	0.4-0.6m
	1997,1999,2001		
	All low Alps sites	<i>Dipsacus fullonem</i> flower underside, <i>Echium vulgare</i> , flower head underside, <i>Leucanthemum vulgare</i> flower undersides, <i>Pastinaca sativa</i> umbel undersides	0.5-1.5m
	2008		
Resting	Site 1 & 2	All feeding sites and roosting sites	0.2-1.5m

Resource type	Site	Species	Height range used
	2009		
	Site 1, 2 &3	<i>Melampyrum arvense</i> , <i>Leucanthemum vulgare</i> , <i>Knautia arvense</i> , <i>Trifolium pratense</i> , <i>T. campestre</i>	
	1997,1999,2001	<i>All feeding sites and roosting sites and grass leaf blades</i>	0.2-1.5m

After overnight roosting individuals would move to the upper surfaces of roosting substrates and bask prior to any activity. Daytime basking or resting with closed wings was sometimes combined with nectaring, or individuals would settle on a range of plants usually between 0.2 m and 1.5 m tall, above the average sward height of the grassland areas occupied (0.3 to 0.6m)(Table 2). Almost all observed flight activity at all sites was in open areas, where nectaring, roosting, and resting occurred, even flying females which were followed to egg-laying sites were in open areas and their flight activity was not centred on areas with high hostplant species density (hedges in northern France), though in the low Alps a few females were seen flying slowly around scrubland edges where scrub species were encroaching on grassland.

Males mainly flew to locate females in open areas with a minority flying along the edges of scrub and hedgerows, occasionally interacting with other males in flight, and also flying down to settled and feeding females. Interactions with females resulted in the females either adopting a rejection posture of either closing their wings or of raising their abdomen tip with open wings firmly pressed to the substrate they were on, resulting in the male flying away. In a few instances the female flew off after male persistence.

Although the weather conditions in 2008 and 2009 were not identical, the proportions of time individuals spent on different activities in the two years were similar, but there were significant differences in behaviour between sexes (Fig. 2). Males engaged in flying for a significantly greater time than females ($W = 3$, $P = 0.008$), while females spent more time nectaring and basking than males yet not significantly. Closed wing resting/daytime roosting was also of longer duration in females (Fig. 2).

Egg-laying was observed thirteen times during adult tracking. Females flew around low and isolated bushes with host plants (*P. spinosa*, *C. monogyna*) with rapidly flapping wings searching for a suitable ovipositing site. Females would often land on a host plant for a few seconds, crawling on a leaf with closed wings to inspect suitability. When a suitable site was found, females bent the abdomen towards the leaf and immediately laid eggs. Oviposition lasted about 15 min with regular pauses while batch laying, after which females flew and engaged in resting and feeding behaviour, away from the hostplant.

Activity of both sexes was related to air temperature, solar radiation intensity and windspeed. In bright sunshine (1200 Wm^{-2}) both sexes could be active (feeding and flying) with a minimum air temperature

of 13 °C, but in cloudy conditions the minimum temperature for male flight activity was 14 °C (solar radiation intensity 200 Wm⁻²) and for females 15 °C with solar radiation > 250 Wm⁻². These minimum environmental conditions for 2008 and 2009 for flight activity are also consistent with the minimum temperature conditions for flight in the low Alps, with both males and females flying at 14 °C and solar radiation at 750 Wm⁻² (14 °C was the lowest recorded air temperature in the low Alps studies). Males initiated open-winged basking in cooler conditions (13°C and 200 Wm⁻²) than females (14°C and 250 Wm⁻²). Once flight and basking are possible then individuals were also recorded feeding.

Flight activity is essential for all other activities and in both sexes flight durations increased with increasing air temperature and solar radiation intensity but increasing wind reduced flight activity. Many flights were of short duration, but some individuals of both sexes made long duration (and distance) flights, including flights of over c.200 m length in straight lines over resource free patches (cereal fields) before they were lost to observation. Night-time roosting commenced with decreasing light levels, irrespective of temperature. This activity was recorded on sunny days when solar radiation intensity decreasing below c. 600 Wm⁻² at c.16:00–17:00 hr even on days when air temperatures were above 23 °C.

Weather conditions affected the behavioural activities of both sexes of *A. crataegi*, with a significant difference on the effect of solar radiation on feeding initiation between sexes ($t = -0.82$, $p = 0.02$), where females fed at significantly higher solar radiation levels (> 250 Watts m⁻²) than males (> 200 Watts m⁻²). Furthermore, females appeared to bask at significantly higher solar radiation intensity (> 250 Watts m⁻², $t = 2.25$, $p = 0.03$), and temperatures (> 14°C, $t = -3.05$, $p = 0.003$) compared to males (> 200 Watts m⁻² and 13°C). Egg-laying was only observed when air temperature was > 23 °C. Flight initiation in females occurred at greater solar radiation intensities ($t = 5.25$, $p < 0.0001$) and temperatures than males ($t = 2.035$, $p = 0.04$). Females engaged in flying at a minimum temperature of 15°C and solar radiations greater than 250 Watts m⁻², while males were recorded flying at 14°C and 200 Watts m⁻². Females also showed to rest at significantly greater solar radiation intensity ($t = -3.33$, $p = 0.003$) and air temperatures ($t = -9.50$, $p < 0.0001$) compared to males. Models showed that flight duration in both sexes was positively affected by solar radiation (F-M: $p < 0.0001$) and air temperature (F-M: $p < 0.0001$), while it was significantly reduced at increased wind speeds (F: $p < 0.0001$; M: $p = 0.049$)(Fig. S1).

Egg-laying site microhabitat selection

In 2008, females were observed laying eggs in the central part of the day with air temperature > 23 °C. In 2009, only one female was observed egg-laying. This female was c.500 m away from the nearest area of activity and after selecting an isolated small *P.spinosa*, it deposited 75 eggs on a leaf upper side at a height of 0.3 m. A total of 50 egg batches were found during the 2008 study period, predominantly on *P. spinosa* ($n = 45$) and occasionally on *C. monogyna* ($n = 5$), with most being placed on south facing leaves ($\chi^2 = 9.68$, $p < 0.01$) and always on the upper side of the leaves. Eggs were laid on significantly smaller plants (height: $U = 703.5$; $p = 0.002$; width: $U = 829$, $p = 0.02$) compared to the unoccupied control plants.

Approximately 50% of egg batches were found on young hostplants between 0.5-1.5m high although almost 65% of available host plants were > 2m high. Furthermore, egg-laying females preferred isolated host plants or those in defunct and gappy hedgerows ($\chi^2 = 17,79$, $p < 0.01$). Only 5 egg-batches were found in 2009, none were in or adjacent to the main areas of activity, but all on isolated small plants and placed between 0.4 and 1m high on southerly facing aspect leaves.

Butterfly abundance and resource characterization

In both the 2008 and 2009 studies, males were more frequently encountered, marked and recaptured than females. Marked individuals were detected up to 17 days after initial marking, together with movement of individuals between patches. In all locations most adult activity was in species rich areas of vegetation, with abundant preferred nectar sources. These areas also had areas of bare ground, with variable % composition of grasses and herb species. (Table 2).

We found that nectar abundance had a significant effect on butterfly abundance ($p = 0.007$) in the studied patches, while no other vegetation factors did. Similarly, the resource-based habitat analysis revealed that population size of *A. crataegi* was positively affected by percentage of host plants ($\beta = -0.418$, $z = -2.589$, $p = .010$) (Fig. 3a) and of nectar plants ($\beta = 1.337$, $z = 5.910$, $p < .001$) (Fig. 3b) but not overall species richness (Fig. 3c). Population size of *A. crataegi* was also positively associated with a heterogeneous distribution of host resources ($\beta = 2.969$, $z = 4.005$, $p < .001$) (Fig. 3d), where host plants were abundant in some areas but scarce or absent in others. In contrast, the distribution of nectar plants showed the opposite pattern whereby butterfly population size was significantly greater in areas where nectar plants were evenly distributed over the site ($\beta = -6.792$, $z = -4.409$, $p < .001$) (Fig. 3e). In addition, adult *A. crataegi* were more abundant at sites with greater spatial overlap between host and nectar plants, significantly increasing the butterfly population size ($\beta = 1.795$, $z = 2.377$, $p < .05$) (Fig. 3f).

Discussion

We observed significant differences in activity engagement between females and males of *A. crataegi*, confirming previous work on this species (Jugovic et al. 2017a). This is also largely in line with evidence on other butterfly species showing a propensity in males to engage in more frequent and longer flights, conceivably to detect receptive females, which take shorter flights and spend more time resting and feeding (Evans et al. 2020; Popović et al. 2022).

Consistent with expectations, oviposition was observed predominantly on *Prunus spinosa* and *Crataegus monogyna*, which have been shown to be the favoured larval hostplant in other European regions (Baguette et al. 2000; Jugovic et al. 2017b, a; Jugovic and Kržič 2019). Interestingly, we found that females significantly preferred to lay eggs on small, isolated plants growing away from hedgerows and at locations away from the main population centres. Available evidence highlights similar behaviours in *A. crataegi*'s larvae, which were found to prefer smaller, young, shrubs with greater sun exposure (Baguette et al. 2000; Jugovic et al. 2017b). A possible explanation for this microhabitat choice for

oviposition is that young, isolated bushes provide better resources for developing larvae, especially as eggs are laid fairly low down and the southerly aspect chosen provides warmer conditions for developing eggs, which may be absent at the basal parts of mature (and managed) hedgerows. Such optimal conditions may be easier to detect with isolated plants than with a continuous hedgerow.

Availability of food and host plant resources are strong determinants of butterfly population abundance (Curtis et al. 2015). Our results support this idea as *A. crataegi* occurred at higher density in areas with high nectar source and host plant abundance and were positively affected by a greater overlap of these resources. Most activity was in areas of vegetation with a relatively high % cover of herbaceous plants and with small amounts of bare ground, and our data indicates that within these areas they tended to avoid microhabitats with a high % cover of grasses, and the preferred patches had a consistent modal height range of 0.3 to 0.6 m and a maximum height range of from 0.4 to 0.8 m. The positive response of butterfly abundance to a heterogeneous distribution of host plants may conceivably align with female preference for scattered bushes as opposed to continuous, linear hedges containing *Prunus* and *Crataegus* species. Flying females which were followed to egg-laying sites were in open areas and their flight activity was not centred on areas with high hostplant species density such as hedgerows around the field. Additionally, we show strong evidence that this species is highly specialised in its use of nectar sources, using mainly purple flowers of *Symphytum uplandicum*, *Trifolium pratense*, *Centaurea nigra*, *Vicia cracca*, *Cirsium arvense*, *Melampyrum arvense*, *Anacamptis pyramidalis*, *Vicia sativa*, *Knautia arvense*, *Echium vulgare* and *Ballota nigra*.

Hence, the optimal habitat appears to comprise grassland areas with consistent availability of food resources and scattered patches of host young host plants.

Furthermore, *A. crataegi* revealed a level of specificity in roosting sites requirements, which are generally tall plants emerging above the general sward height. We only found roosting occurring on the undersides of flowers of *Leucanthemum vulgare*, *Dipsacus fullonem*, *Pastinaca sativa* and *Echium vulgare*. The selection of these plants might be associated with predator avoidance by visual crypsis and position as seen in other species (Wiklund and Tullberg 2004) and also serving as sites where individuals can walk short distances to bask on the upper sides of these substrates prior to activity.

As in most ectotherms, weather conditions play a crucial role in determining butterfly behaviour, due to reliance on external sources to reach optimal thoracic temperatures to enable flight and other activities (Ohsaki 1986; Wenda et al. 2021). Our results support these findings as weather conditions were found to have an impact on the activity of *A. crataegi*. Behaviours such as flight, which is essential for locating mates, hostplants, nectar sources, roosting sites, and egg-laying sites, and other resource patches did not occur below 15°C (females) and 13°C (males), and only then in bright sunshine (1200 Wm^{-2}). Under cloudy conditions, solar radiation levels of 200 Wm^{-2} for males and 250 Wm^{-2} for females, and air temperatures $> 14^\circ\text{C}$ for males and $> 15^\circ\text{C}$ for females are required. Flight durations increase with increasing solar radiation, which could explain the observations of the species' range expanding to

higher elevations (Merrill et al. 2008), as it appears to be more strongly dependent on solar radiation than on temperature to initiate flight.

Conservation and reintroduction implications

This multi-year study provides novel insight of the fine-scale microhabitat and climatic requirements of *A. crataegi*, which are key to inform species conservation strategies. Our results suggest that *A. crataegi* is highly selective in the use of nectar sources, has specific roosting requirements and deposits eggs on young small hostplants with southerly aspects. We have also demonstrated that most adult activity occurs in grassland areas that are rich in herbaceous species, but within such areas, the butterfly is selective in the height of vegetation it uses, and it preferentially uses areas where grass cover is relatively low. Our Mark-Release-Recapture supports previous evidence (Baguette et al. 2000; Lind et al. 2007; Jugovic et al. 2017a) and indicates that *A. crataegi* is highly mobile and able to traverse resource-free zones (i.e., cereal fields) in search of alternative patches. Evidence of residence time of individuals within resource rich patches was low, with a minority of marked individuals moving at least 200–500 m between resource rich patches. This species can therefore be described as having characteristics associated with early successional habitats and fragmented patches (Dennis et al. 2003; Dennis 2004). This is a crucial aspect to be considered when planning conservation strategies as *A. crataegi* is likely to create meta-populations and consequently require a landscape scale approach (Thomas et al. 2025). This signposts a model for the reintroduction for this species involving multiple sites separated by distances that allow for meta-populations to establish and where simultaneous releases are conducted over consecutive years.

Overall, we found that *A. crataegi* requires resources that tend to occur in species rich grassland and woodland edge but where both are adjacent and where there is also some disturbance (e.g. grazing/cutting). In the British Isles, many of the plants used are associated with damp meadows and others are short lived perennials that require disturbance. Likewise for egg-laying, there is a dependence on hostplants spreading out from existing areas of woodland or hedgerows into grassland. This matrix of different plant communities does not comprise a priority habitat type, and where it does occur, it is usually short-lived, representing an ephemeral plant community. We therefore suggest that if *A. crataegi* is re-introduced into the British Isles, it needs to be introduced in locations where there is some periodic disturbance, and multiple patches of varying successional stages. Changes to agri-environment subsidies in the British Isles to focus on delivering biodiversity benefits and public goods, combined with an increase in low-intensity farming and some rewilding (an approach to land management that allows natural processes to lead) may provide new opportunities for *A. crataegi* especially if the value of periodic disturbance is incorporated into such schemes.

Declarations

Conflict of interests:

The authors declare no conflict

Author Contribution

T.B., T.S., F.Ra., and K.H. conceived ideas and designed the methodology for the 2008 season; T.B., T.S. and E.P. conceived ideas and designed the methodology for the 2009 season; F.Ra. H.W., A.N.K., S.R. and F.R. conceived ideas and designed the methodology for the 2024 season; F.Ra., E.P., H.W. and A.N.K. collected the data, F.Ra., E.P., H.W. and A.N.K. analysed the data; H.W., A.N.K. and F.Ra. led the writing of the manuscript with input from all authors. All authors gave their final approval for publication.

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Data Availability

The data that support the findings of this study will be available at DRYAD (link to be generated)

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Figures

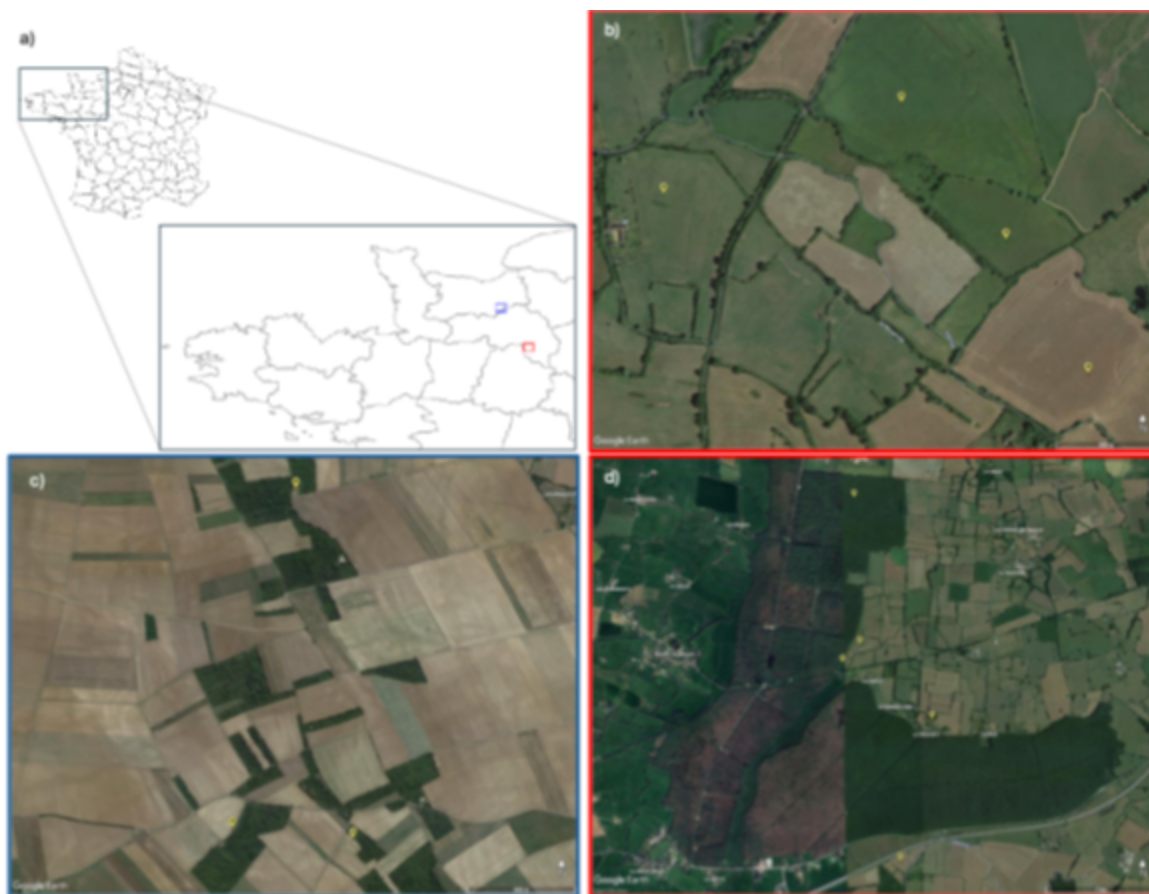


Figure 1

Map of the study sites. (a) Study area located in the North of France, specifically in the region of Orne (red square) and Calvados (blue square). (b) Location of the study sites used in 2008, comprising wet

meadows and grasslands (c) Location of the study sites used in 2009, consisting of isolated mosaic of small woods, shrub edges and grassland patches in large agricultural plains; (d) Location of the study sites used in 2024, comprising wet meadows, grasslands and private gardens.

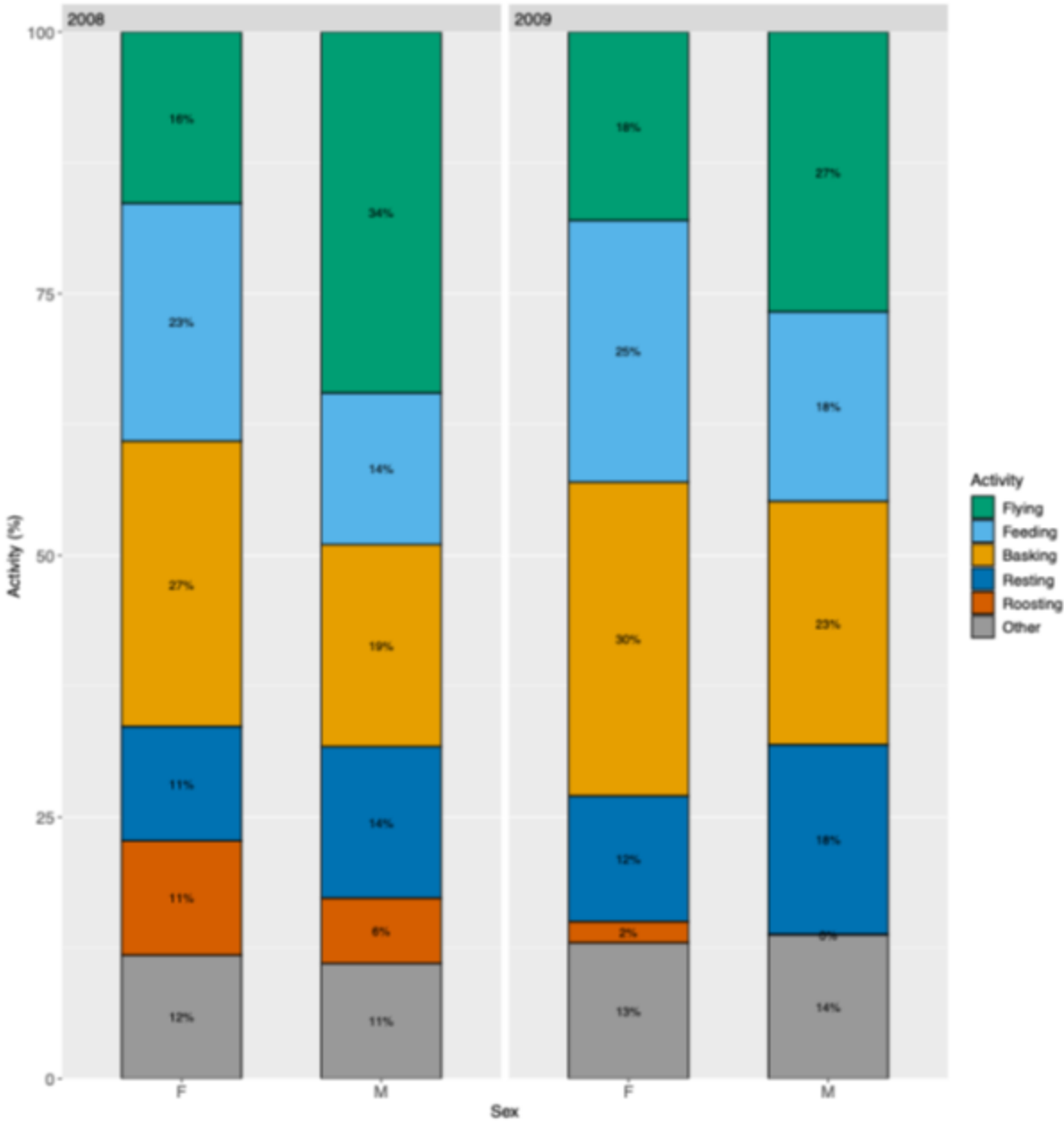


Figure 2

Diurnal time-activity budget of *A. crataegi* divided by sex (F, female; M, male) in the 2008 sites (left) and the 2009 sites (right). Six main categories of behaviour were identified as basking, feeding, flying, resting, roosting and other (e.g. copula, courtship)

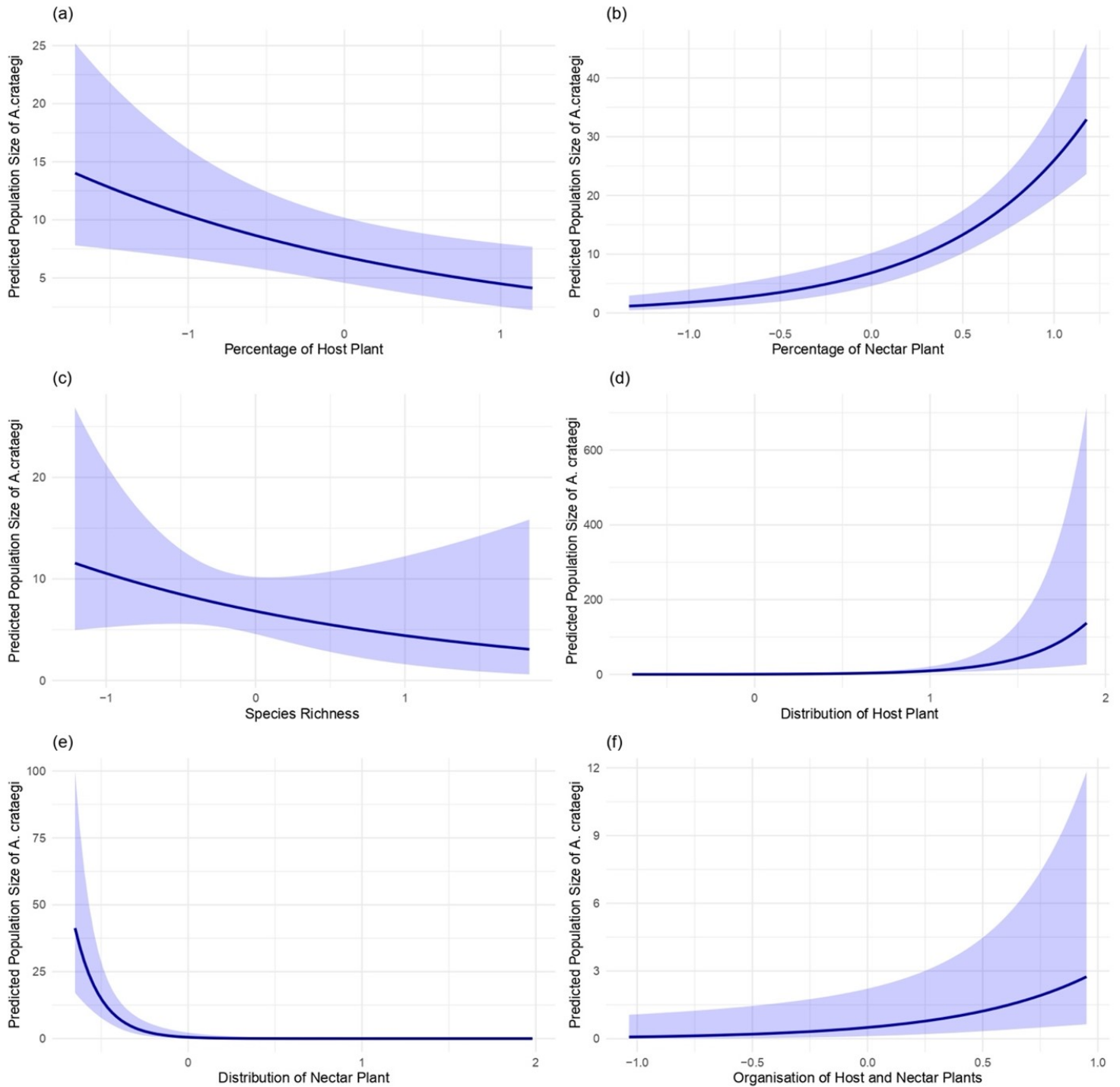


Figure 3

Predicted population size of *A. crataegi* in relation to environmental variables; (a) percentage of host plants (b) percentage of nectar plants (c) species richness (d) distribution of host plants (e) distribution of nectar plants (f) resource organization. Dark lines are predictions, shaded areas are 95% confidence bands, derived from the GLMs analysis.

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