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REVIEW PAPER

The biology and ecology of the large blue butterfly *Phengaris (Maculinea) arion*: a review

Matthew P. Hayes[1]

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Abstract It has long been known that *Phengaris (Maculinea) arion* has a complex lifecycle involving the social parasitisation of ants. However, research triggered by the extinction of the original UK population of *P. arion* in 1979 has greatly enhanced our knowledge of this butterfly. Adults lay their eggs on *Thymus* spp. and ovipositional patterns seem to be dictated by host plant bud phenology and be independent of host ant presence. After feeding for around 3 weeks *P. arion* larvae fall to the ground and await adoption by host ants of the genus *Myrmica*. To achieve adoption *P. arion* larvae employ various forms of appeasement and mimicry, of which chemical and acoustic mimicry seem to be especially important for gaining colony integration and raising larval status respectively. The predatory larvae of *P. arion* then proceed to eat their host ants' brood until they are ready to pupate. In the UK *P. arion* appears to be restricted to one primary host ant, *Myrmica sabuleti,* but across Europe a more complex pattern of host ant use seems to be occurring. In the UK the niche of *M. sabuleti* consists of closely cropped grassland and it is thought that a decline in these areas led to the extinction of *P. arion* in 1979. Scrub clearance and the implementation of grazing regimes has since enabled the successful reintroduction of *P. arion* to the UK, where sites are maintained to allow high densities of the specific larval host plant and host ant to co-occur.

Keywords *Phengaris arion* · *Myrmica sabuleti* · Social parasitism · Ovipositional cues · Host mimicry · Host ant specificity · Ecological niche · Micro-climate

Introduction

Phengaris arion is an obligate social parasite with a complex life-cycle involving initial oviposition on a host plant, followed by adoption into an ant nest during its final larval instar (Thomas et al. 1989). The basic lifecycle of *P. arion* has been known for a long time (Chapman 1916a, b; Frohawk 1906, 1916). However, despite this knowledge, the original UK population of *P. arion* underwent decline for most of its documented history (Thomas 1977). Numerous conservation attempts failed to encourage population persistence, indicating that the precise conditions needed to maintain a viable population of *P. arion* were not understood (Thomas 1980). In 1972, when numbers were critically low, it was decided that intensive study of the butterfly's ecology was needed to ascertain what vital information was being missed. This research, headed by Dr Jeremy Thomas, has since lead to crucial advances in our understanding of the butterfly's needs (Barnett and Warren 1995).

Unfortunately, findings came too late for the UK population, which became extinct in 1979 (Thomas 1980). However, our increased understanding of the butterfly's ecology has since allowed its reintroduction to the UK from Swedish stock populations and should help enable the implementation of effective conservation methods in the future (Barnett and Warren 1995). This review aims to outline our current understanding of the biology and ecology of *P. arion* throughout the different stages of its life cycle.

✉ Matthew P. Hayes
matthewhayes@hotmail.co.uk

[1] School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, UK

Phylogeny of the genus *Phengaris*

The genus *Phengaris* is one of the most extensively studied insect groups in the world (Settele et al. 2005). Despite this, the taxonomic status of species within the genus and their phylogenetic relationships are still unclear, as demonstrated by the recent suggestion that *Phengaris* should subsume the genus *Maculinea* (Fric et al. 2007). Of the species previously belonging to *Maculinea*, five are commonly recognised in Europe: *Phengaris arion*, *Phengaris teleius*, *Phengaris nausithous*, *Phengaris alcon* and *Phengaris rebeli*, with a sixth species, *Phengaris arionides*, recognised in East Asia. A few other Asiatic species such as *Phengaris kurentzovi* and *Phengaris cyanecula* have also been proposed but have undergone relatively little study (Als et al. 2004).

Several genetic analyses suggest that some of the commonly recognised species lack sufficient differentiation to be considered separate taxa, whilst others may encompass enough variation to be divided further. Als et al. (2004), Pech et al. (2004) and Ugelvig et al. (2011b) found that *P. alcon* and *P. rebeli* show little genetic divergence and suggest that they are instead two ecological forms of one species. Czekes et al. (2014) similarly found no distinct morphological or genetic differences between the two putative species but concluded that clear ecological and behavioural differences warranted the conservation of both intraspecific forms.

In contrast, Als et al. (2004) and Ugelvig et al. (2011b) found significant genetic structuring within the three other European *Phengaris* spp., suggesting that additional cryptic species may be represented within *P. teleius, P. nausithous* and *P. arion*. *P. arion* exhibits quite extensive morphological variability over its European range, with upwards of 20 forms being described and three sub-species commonly recognised (Bereczki et al. 2014). Two of these sub-species, *Phengaris arion arion* and *Phengaris arion ligurica,* also known as Spring and Summer *P. arion* respectively on account of their differing flight periods, both occur in the Carpathian Basin in East Central Europe. Bereczki et al. (2014) undertook a multilevel study comparing the differentiation of syntopic populations of these two forms and found discordant results for genetic and morphological patterns. Significant morphological differences were found in wing and male genital traits but allozymes and mitochondrial loci lacked significant differentiation. Bereczki et al. (2014) noted that infection of the *P. arion* populations with intracellular *Wolbachia* bacteria may have been partially responsible for the discordant results. *Wolbachia* bacteria can modify their hosts' reproductive behaviour to better transmit themselves down the female line. This enables the bacteria to sweep across populations, along with any maternally inherited organelles such as mitochondria, which can reduce mitochondrial diversity and cloud evolutionary patterns. However, despite 100 % of *P. arion* samples in the Carpathian Basin being found to be infected with a single strain of *Wolbachia* bacteria, no evidence of such a selective sweep was discovered (Bereczki et al. 2015). Therefore, although differences in male genitalia may indicate incipient prezygotic isolation (Bereczki et al. 2014), genetic similarity suggests that the different forms of *P. arion* do not yet represent separate species.

Biogeography of the genus *Phengaris*

The geographic distribution of parasitic genera such as *Phengaris* is interesting as the most diverse lycaenid faunas tend to exist in humid, tropical regions, whilst parasitic taxa appear to be restricted to regions with pronounced unfavourable seasons. Fiedler (1998) suggests that this distribution may indicate that a long unfavourable season is key for providing a selective pressure towards the parasitisation of ants. Larvae seeking shelter in the more tolerable microclimate of an ants' nest could promote increased intimacy in close confines and perhaps produce the conditions required to lead first to mutualism and then parasitisation of the ants by *Phengaris* spp. Records of non-parasitic larvae sheltering in ant nests support this theory (Fiedler 1998).

The genus *Phengaris* belongs to the Glaucopsychiti subtribe, which is most diverse in Eastern Asia. Furthermore, no Glaucopsychiti genus is endemic to Europe, whereas some are entirely Asiatic. Taken together, this information suggests that the subtribe and *Phengaris* genus originated from East Asia (Fiedler 1998). In this scenario the last common ancestor of *Phengaris* spp. likely evolved in the Asian Palearctic where a long unfavourable season constrained the climate and host plant availability, driving the taxa to associate with ants and evolve parasitic lifestyles. The European *Phengaris* spp. then secondarily colonised the western parts of their ranges, following the open–steppe like habitat required by their *Myrmica* spp. host ants. This prevented them penetrating far into arboreal forests or into Mediterranean regions, explaining the current biogeography of the genus, restricted to the Palearctic with its long unfavourable season (Fiedler 1997).

Choice of larval food plant

Adult *P. arion* emerge in late June/July and lay their eggs on the flower buds of their larvae's food plant. The eggs hatch after 7–10 days and the larvae spend around 3 weeks feeding on the plant (Thomas 1977). All *Phengaris* spp.

larvae are narrowly oligophagous or even monophagous on specific host plants (Fiedler 1998) and *P. arion* limits its oviposition to closely related *Thymus* and *Origanum* spp. (Elmes and Thomas 1992). *P. arion* has been found to oviposit on numerous *Thymus* spp. across its European range including: *Thymus drucei* (Thomas 1977), *Thymus serpyllum* and *Thymus pulegioides* (Sielezniew et al. 2005). *Thymus* spp. are preferentially used for oviposition but *Origanum vulgare* can be exploited in its absence (Griebeler 2011). For example, in 1992 a drought in Oland, Sweden caused virtually all *Thymus* spp. to fail and almost all *P. arion* eggs were instead laid on *Origanum vulgare*. Larval survival was reduced, but the population persisted and was able to recover when conditions returned to normal (Thomas and Simcox 2005).

In addition to host plant specificity, adult *Phengaris* also restrict their oviposition to a particular short-lived phenological bud stage (Thomas and Elmes 2001). Patricelli et al. (2011) observed that when all bud stages of a suitable host plant were available, *P. arion* preferentially chose to lay eggs on slightly immature buds. This was also observed by Musche et al. (2006) who additionally noted that *P. arion* avoided ovipositing on the smallest flower heads. Large flower heads provide more resources for the larvae and selection of the slightly immature phenological stage helps ensure that the larvae have enough time to feed and develop before the bud expires (Musche et al. 2006).

Is choice of oviposition site mediated by host ant presence?

P. arion larvae quickly progress through their first three instars and upon reaching their fourth and final instar they desert their host plant and drop to the ground. The larvae are then adopted by foraging worker ants of the genus *Myrmica*, who carry them back to their nest. Once inside the nest *P. arion* larvae proceed to predate and feed on the ants' brood and after around 9 months the larvae pupate; with the adults emerging a few weeks later to repeat the cycle (Thomas 1977). Thomas and Elmes (1998) suggest that in order for *P. arion* populations to persist, at least 50 % of their eggs must be laid within the range of host ant species. The early larval instars of *Phengaris* spp. are poor dispersers and are therefore entirely dependent on the adults selecting a suitable oviposition site (Patricelli et al. 2011). A weak larval dispersal ability and obligate dependence on *Myrmica* spp. might suggest that *P. arion* would greatly benefit from choosing oviposition sites based on host ant presence. However, there has been a long-term controversy over this issue (Furst and Nash 2010).

One argument for ant-related oviposition is that some studies suggest this behaviour is exhibited by other European *Phengaris* spp. Van Dyck et al. (2000) looked into the presence of this behaviour in *P. alcon*. They found that host plants surrounded by suitable host ant nests received significantly more eggs than those outside of the ants' foraging range. Wynhoff et al. (2008) found similar results for *P. teleius* and *P. nausithous* and they suggest that the presence of widespread host plants in relation to relatively rare host ants would produce many population 'sinks' if adults were to oviposit randomly on all suitable host plants. Under these circumstances adult *Phengaris* may need to detect host ant presence to ensure the long-term fitness of their larvae. This supports the idea of *Phengaris* spp. adopting ant-related oviposition patterns. However, many studies contradict the findings of these papers. Furst and Nash (2010) suggest that the ovipositional niche of *P. alcon* is much more closely tied to the phenological stage of their host plant than to the presence of their host ants. Thomas and Elmes (2001) also found that for all five European *Phengaris* spp. their patterns of oviposition are best explained by variation in plant phenology and are random with respect to host ant presence.

Papers regarding ant-mediated oviposition in *P. arion* also vary in their conclusions. Patricelli et al. (2011) placed ant pitfall traps at a study site with wide ranging larval host plants and scattered *Myrmica* spp. nests. They found a positive correlation between the number of ants in the pitfall traps and the likelihood of *P. arion* eggs being laid nearby. However, Patricelli et al. (2011) once again highlighted the strong importance of host plant bud phenological stage in determining oviposition site. Thomas and Elmes (2001) suggest that selecting for host plant phenological stage may itself produce ovipositional patterns that appear to be ant-mediated. They argue that variation in microhabitat across heterogeneous sites can determine both when host plants flower and the spatial distribution of *Myrmica* spp. Therefore, host plants in the same microclimatic conditions should develop the same phenological bud stage at the same time and due to specific climatic preferences of *Myrmica* spp., plants in a given microclimate are also likely to co-exist primarily with one particular *Myrmica* species. Therefore, by laying eggs on a specific phenological bud stage, *P. arion* oviposition could primarily occur in the range of one *Myrmica* species and appear to be ant-mediated when it is in fact not (Thomas and Elmes 2001).

Alternatively, ovipositional cues such as suitable bud phenology and vegetation structure could be utilised by adult butterflies indirectly to locate the presence of a micro-niche suitable for their host ants. For example, *P. teleius* and *P. nausithous* feed on the same host plant but exploit different species of ant (Thomas and Elmes 2001). It was found that by selecting different phenological bud stages on the same dates, eggs of both species were primarily laid in the foraging range of their host species of *Myrmica*, as the preferred growth stage of each butterfly developed in a vegetation structure also preferred by their host ant species (Thomas and Elmes 2001). In other words ovipositional cues used to select a suitable host plant also indirectly selected sites that were suitable for their required host ant. Therefore, adult *Phengaris* indirectly selecting a site's suitability for a host ant seems like a plausible alternative to direct ant detection. Furthermore, this would result in suitable sites not always containing host ants but being more likely to do so, which could explain why some studies have observed ant-related oviposition and others have not.

Several studies have also explained potential disadvantages with ovipositing in direct relation to ant presence. Many *Myrmica* spp. occupy very similar niches with overlapping spatial and temporal ranges and will all adopt larvae of *P. arion* if they come across them (Thomas 2002). Therefore, many species of *Myrmica* can forage below the same host plant even if it is very close to a specific host ant's nest. This means it may not be worth selecting oviposition sites based on the presence of one host ant species, as workers of other species are still quite likely to adopt the larvae (Thomas 2002). Another problem that could arise from laying many eggs close to host ant nests is high density-dependent mortality of the larvae. With many larvae in the same area, or even on the same plant, intraspecific competition may be extremely high. For example, the mass of *P. alcon* larvae when leaving their host plants is significantly lower when larvae are at higher densities (Gadeberg 1997, cited by Van Dyck et al. 2000). Density-dependent mortality is an even greater issue once larvae are adopted into ant nests, especially for species such as *P. arion*, which inefficiently feed by directly consuming the ant brood (Thomas and Elmes 2001). Having many larvae in one nest can lead to the early exhaustion of their food resource and intense scramble competition, decreasing overall survival probability (Musche et al. 2006). Van Dyck et al. (2000) suggested that adult *Phengaris* may be able to detect high egg loads on a plant and therefore avoid overcrowding. In their study they found that towards the end of the flight season *P. alcon* laid significantly more eggs on plants with no host ants in their vicinity. This temporal change in oviposition preference supports a density–dependent shift, whereby oviposition may initially be ant-mediated but when high egg density is reached eggs may be laid further away from the host ants to avoid intense competition (Van Dyck et al. 2000). Similar results have also been found for *P. teleius,* along with the first potential evidence of oviposition deterrent pheromones being used as the mechanism by which a more even egg distribution is achieved. Sielezniew and Stankiewicz-Fiedurek (2013) found that *P. teleius* avoided ovipositing on flower heads that had previously been visited by conspecific females. The adult females exhibited very stereotyped behaviour, using their antennae, legs and abdomen tip to examine potential oviposition sites. If oviposition took place they then proceeded to spend time touching the flower head with their antennae and abdomen tip, whereas rejection of a flower head was a much faster process. This behaviour suggests that pheromone detection and marking may be used to deter conspecific oviposition and intense larval competition (Sielezniew and Stankiewicz-Fiedurek 2013). However, other studies have failed to show temporal shifts in *Phengaris* spp. oviposition behaviour. Wynhoff et al. (2015) found that for *P. alcon* there was no indication that oviposition on plants lacking host ant nests in their vicinity altered over time. Thomas and Elmes (2001) also found no evidence of a temporal shift in *P. arion* egg distribution due to egg crowding. Therefore, *P. teleius* may use oviposition deterrent pheromones but more study is needed to ascertain the properties of this hypothetical marker. Further research should also be undertaken into whether such pheromones are used by the other *Phengaris* spp., especially *P. arion,* which appears to carry out much shorter oviposition trips that do not suggest marking (Sielezniew and Stankiewicz-Fiedurek 2013). *P. arion* may improve its larvae's survival chances by simply ovipositing randomly in relation to host ants, thereby reducing crowding and intense competition.

A final issue arises when considering how adult *Phengaris* might be able to detect the presence of host ants. It has been speculated that visual cues would be an unlikely method of detection as *Myrmica* spp. colonies can be nearly invisible in vegetation (Musche et al. 2006). Van Dyck et al. (2000) concluded that any method of direct detection had its issues, but that olfactory pheromone cues may be most likely, a conclusion with which others agree (Furst and Nash 2010; Patricelli et al. 2011). This is supported by the fact that social insects produce arrays of pheromones for colony organisation and recognition (Musche et al. 2006). However, Thomas and Elmes (2001) argue that the explanations for direct ant detection proposed by Van Dyck et al. (2000) are unconvincing. Ant pheromone trails are short-lived and the peak oviposition time of *Phengaris* spp. differs from the peak foraging time of *Myrmica* spp. When the adult *Phengaris* are laying their eggs, most of the *Myrmica* spp. workers will be underground, and their short-lived odour trails may no longer be detectable. In addition, *Myrmica* spp. seldom ascend host plants, meaning that their trails may almost entirely be restricted to the ground, where it is even less likely that adult *Phengaris* will detect them (Thomas and Elmes 2001). Musche et al. (2006) tested the hypothesis that female *Phengaris* used pheromone cues to detect ant presence and found no evidence of this behaviour.

Myrmica rubra is the host ant of *P. nausithous* and, like all *Myrmica* spp., *M. rubra* creates a specific colony odour, which also marks the soil of the nest (Musche et al. 2006). A selection of host plants were covered in soil from *M. rubra* nests to see if female *P. nausithous* would preferentially oviposit on them. No correlation was observed; instead, once again, size and phenology of flower heads accounted for observed egg distributions (Musche et al. 2006).

Much of the literature suggests that ant-related oviposition in *P. arion* and *Phengaris* spp. in general does not occur (Thomas and Elmes 2001; Furst and Nash 2010) and when it has been observed other factors can also explain oviposition patterns (Patricelli et al. 2011). Host plant bud phenology seems to offer the best explanation for the majority of observed oviposition patterns. It may be that, alongside factors such as vegetation structure, these ovipositional cues act indirectly to signal the environment's suitability for host ants, but direct host ant detection seems less likely (Thomas and Elmes 2001). Furthermore, direct ant-related oviposition may have negative effects on larval survival and no convincing method of ant detection has yet been described for *Phengaris* spp. (Musche et al. 2006).

Adoption into host ant nests

In order for *P. arion* larvae to survive their 4th and final instar they must first be adopted by a host ant and be transported back to their nest. Once there the larvae must then avoid aggression and gain integration into the colony (Van Dyck et al. 2000). *Phengaris* spp. larvae achieve this by employing numerous methods of appeasement and mimicry (Elmes et al. 2001).

Upon reaching their 4th instar the larvae of *P. arion* time leaving their host plant so that they fall to the ground during the peak foraging time of their host ant species, increasing the chances of a host ant worker quickly coming across them (Thomas 2002). The larvae of *P. arion* also possess a very strange growth pattern whereby they progress through their first three larval instars quickly and obtain only around 2 % of their final body mass (Elmes et al. 2001). Reduced early growth means that upon leaving their host plant *P. arion* larvae are still very small, allowing them to be easily transported by the worker ants of *Myrmica* spp. In addition, the small larvae are of a similar size to the *Myrmica* spp. ant grubs (Elmes et al. 2001). This morphological mimicry is thought to help trick the ant workers into thinking they have come across one of their own escaped brood (Thomas 2002). Having undergone slow initial growth to aid integration into their host nest the *P. arion* larvae then grow extremely rapidly to make up for this deficit and gain sufficient size before pupation (Elmes et al. 2001).

The 4th instar larvae of *P. arion* also possess highly developed ant-associated epidermal organs including a prominent Dorsal Nectary Organ (DNO) as well as an increased density of Pore Cupola Organs over their dorsal surface (Sliwinska et al. 2006). The Dorsal Nectary Organ produces droplets of a sugar-rich secretion, which are sometimes offered to ants during the adoption process (Sliwinska et al. 2006). DNO secretions are not thought to attract ant workers from a distance (Thomas 2002) but upon discovery may help to pacify ants and maintain their attendance (Barbero et al. 2012). When discovered, *P. arion* larvae can be examined and 'milked' for upwards of an hour before adoption occurs (Thomas 2002). After extensive examination the larvae then rears up into an S-shape, contracts its body and causes its thoracic segments to swell. Turgidity is thought to be another cue by which *Myrmica* spp. workers recognise their brood (Thomas 2002) and this signal finally induces adoption, causing the attending ant worker to seize the *P. arion* larvae and carry it back to its nest (Thomas 1977).

Chemical mimicry

Although many signals are thought to play a role in the initial adoption of *Phengaris* spp. larvae, the importance of chemical communication for nest mate recognition between ants has led some to suggest that chemical mimicry is likely the main method used by larvae to gain prolonged integration into a colony (Elmes et al. 2002). Semiochemicals are used by ants for inter-individual nestmate recognition, with hydrocarbons on the cuticle thought to be the main chemical cue. Discrimination is based on the ants comparing the chemical profile of other individuals with their own template and judging overall similarity (Lenoir et al. 2001). Within the colony, individuals share their recognition cues to form a 'uniform odour blend' or gestalt odour. This allows altruistic behaviours to be directed towards nest-mates with a similar gestalt odour and rejection of alien conspecifics with dissimilar odours. Once adopted, *Phengaris* spp. must therefore blend into a colonies gestalt odour by achieving some degree of chemical similarity with the host ants or else suffer rejection (Lenoir et al. 2001). They are thought to achieve this in two ways. One method is by actively biosynthesising the hosts' cues (Akino et al, 1999), which are most probably produced by the Pore Cupola Organs that are present in high densities on *Phengaris* spp. larvae in their 4th instar (Elmes et al. 2001). The other method is chemical camouflage; whereby the chemical cues are acquired from direct contact with the host ants (Akino et al. 1999). Preadopted larvae have not yet been in contact with their host ants so biosynthesis is likely used to create a simple hydrocarbon profile that roughly mimics their host ant species (Schlick-Steiner et al. 2004). Then, in order to develop the full gestalt odour of a specific colony it is thought that a combination of chemical camouflage and some further biosynthesis may be used (Schonrogge et al. 2004). Solazzo et al. (2015) found evidence that the hydrocarbon tetracosane may be particularly important in promoting initial contact between *P. nausithous* larvae and their host *M. rubra*. However, tetracosane does not appear to trigger the complete adoption process, which seems to require the full complement of mimetic compounds possessed by *Phengaris* spp. caterpillars.

Acoustic mimicry

In contrast to chemical communication, acoustic signalling has traditionally been regarded as weakly developed in ants. However, it has recently been found that different ant castes produce different calls, which may have a role in signifying status and inducing behaviours in other colony members (Barbero et al. 2012). Both *Phengaris* spp. larvae and adult *Myrmica* ants stridulate to produce acoustic signals and it is now thought that acoustic mimicry may play quite a large role in integrating larvae into ant colonies (Thomas et al. 2010). Barbero et al. (2009a) compared the acoustic signals produced by three *Myrmica* spp. and found no significant difference between them. All three species had significantly different calls between their queen and worker castes but each caste possessed nearly identical calls across all three species (Barbero et al. 2009a). This suggests that acoustic signalling is genus specific and would thus be of little use for kin-discrimination as a given *Myrmica* spp. could not distinguish other species' calls from their own (Barbero et al. 2009a). Instead, queen *Myrmica* are thought to use their calls to reinforce their supreme social status (Barbero et al. 2009a) and this may be used by *Phengaris* spp. larvae to exploit worker castes.

Barbero et al. (2009a) tested this by recording the sounds produced by *P. arion* caterpillars and compared them with the calls of their host ant *Myrmica sabuleti*. They found that the stridulations of *P. arion* larvae most closely resembled those of queen *Myrmica*. Barbero et al. (2009b) found the same result for *P. rebeli,* where acoustic mimicry of the queen was thought to raise larvae's status above that of the ants' own brood, so that when the nest was disturbed *P. rebeli* larvae were the first to be rescued! This elevated status could not be accounted for by other means such as chemical mimicry. Therefore, colony identity is thought to be determined by semiochemicals but hierarchical status is thought to be determined by acoustic signalling (Thomas et al. 2010).

Cuckoo and predatory behaviour

Once inside an ant nest, *Phengaris* spp. can exploit their hosts in two markedly different ways. Species utilising these different methods of host ant parasitisation form two distinct clades within the genus *Phengaris* and are said to adopt either cuckoo or predatory behaviour (Pech et al. 2004). *P. arion* is known as a predatory species as its larvae kill and eat the brood of its host ant. Predatory larvae limit interaction with their hosts by inhabiting peripheral cells in the nest, from which they periodically travel to the brood chambers in order to feed (Barbero et al. 2009a). In contrast, the larvae of *P. alcon* and *P. rebeli* reside in the brood chambers of the ant nest alongside the developing ant grubs. These *Phengaris* are known as cuckoo species as their larvae are fed directly by worker ants via trophallaxis (Schonrogge et al. 2004). In order for cuckoo larvae to make use of this feeding method, which is six times more efficient than eating the ants' brood, they must be able to interact with their hosts regularly without rejection (Patricelli et al. 2011). It has been hypothesised that cuckoo species might achieve this by mimicking their host ants more closely than predatory species do (Elmes and Thomas 1992).

There is some evidence for this being true in the case of chemical mimicry. Analyses by Pech et al. (2007) found that cuckoo species may alter their chemical profiles to match local host ant populations more closely, whereas this was not found for predatory species. It may be that predatory species sacrifice close colony integration to gain a slightly more generalist chemical profile. This could promote larval adoption into a wider number of host ant nests and alleviate some of the intense scramble competition that predatory larvae experience as a result of their inefficient feeding method (Elmes et al. 2002).

However, comparisons of *P. arion* and *P. rebeli* stridulations found both cuckoo and predatory larvae to be equally good at mimicking the acoustics of their host ants (Barbero et al. 2009a). This is surprising as cuckoo larvae use acoustic signals more frequently to gain ant attendance and cuckoo calls elicit more reactions from host ants than the calls of predatory larvae (Sala et al. 2014), which is odd if both produce nearly identical signals (Barbero et al. 2009a). These findings indicate that cuckoo species do not mimic their host ants more closely than predatory species in all respects and this suggests that the link between precise host mimicry and colony integration is not straight forward.

Parasitoid wasps

In addition to relying on two specific larval resources, each *Phengaris* species also appears to support an equally specialised parasitoid wasp. Ichneumonid wasps inject their eggs into the tissues of *Phengaris* spp. caterpillars and each wasp larvae then proceeds to feed on the body of their host, before finally killing the caterpillar at the pupal stage (Settele et al. 2011). Parasitised *Phengaris* spp. caterpillars are reared by their host ants in the same manner as the healthy ones but instead of a butterfly, a single adult wasp emerges after pupation (Hochberg et al. 1996).

As far as is known each parasitoid wasp is host–specific to a single *Phengaris* species, with cuckoo and predatory caterpillars being parasitised by different genera (Tartally 2005). Wasps of the genus *Ichneumon* locate and sting caterpillars of cuckoo *Phengaris* spp. within ant nests, whereas wasps of the genus *Neotypus* sting predatory caterpillars whilst they are still feeding on their host plants. It is thought that these alternative strategies are used by the wasps on account of the different lifestyles of cuckoo and predatory caterpillars (Thomas and Elmes 1993). Predatory *Phengaris* spp. have quite a high chance of exhausting their food supply within ant nests due to their inefficient feeding method and a *Myrmica* spp. nest rarely supports more than one larvae through to adulthood. Therefore, it is a poor strategy for adult wasps to risk entering many heavily guarded ant nests to parasitize only one or two caterpillars within. Instead, stinging numerous unguarded caterpillars whilst still on their food plants will spread wasp larvae more widely between several nests. This increases the chances of some wasp larvae surviving, even if many ant colonies are overexploited and the parasite they are hosting starve (Thomas and Elmes 1993). In contrast the more efficiently feeding Cuckoo larvae tend to emerge from fewer ant nests and in higher densities than those of predatory species. In this case it is a better strategy for adult wasps to risk the attacks of *Myrmica* spp. ants and infiltrate nests containing cuckoo caterpillars. If they succeed they are likely to encounter several hosts with a high chance of survival, which may support their larvae through to adulthood (Thomas and Elmes 1993).

These Ichneumonid parasitoids exhibit extreme behavioural, morphological and physiological adaptations, which enable them successfully parasitise their hosts. *Ichneumon eumerus*, the parasitoid of the cuckoo species *P. rebeli*, systematically searches areas for the chemical odours of *Myrmica* spp. ants and most readily enters the nests of *Myrmica schencki*, showing a clear preference for the main host ant of *P. rebeli* (Hochberg et al. 1998). Amazingly, from the nest entrance *I. eumerus* can then detect whether or not *P. rebeli* caterpillars are present within and only enters nests that contain them. Chemical detection seems unlikely due to *Phengaris* spp. closely mimicking the cuticular hydrocarbon profiles of their host colony. Perhaps the parasitoids can instead distinguish the caterpillar stridulations from those of their host ants, as their acoustic mimicry is less specific (Thomas and Elmes 1993). Upon entering a nest *I. eumerus* releases allomones that cause confusion amongst the *M. schencki* workers and for them to attack one another. The wasp is also heavily armoured and bludgeons past the ants to reach the caterpillars and get back to the surface. Similar adaptations are thought to be possessed by other ichneumonid parasitoids, such as that of *P. arion,* in order for them to escape ant nests upon emergence from their host's pupa (Tartally 2005).

Host ant specificity

Inadequate knowledge surrounding the host ant specificity of *P. arion* is thought to be one of the key reasons why conservation attempts failed for the original UK population. Research has since revealed that *P. arion* is primarily hosted by only one species of *Myrmica* ant in the UK, *M. sabuleti* (Elmes and Thomas 1992). It was previously thought that any ant species of the genus *Myrmica* could successfully host *P. arion* through to adulthood. However, although all species of *Myrmica* will adopt *P. arion* larvae, survival rates differ drastically within their nests (Sielezniew and Stankiewicz-Fiedurek 2008). Therefore, *P. arion* has a much narrower niche than was accounted for in initial conservation attempts and this explains why populations disappeared from apparently suitable sites where food plants and nests of other *Myrmica* spp. were abundant (Elmes and Thomas 1992). Thomas et al. (1989) found evidence indicating similar degrees of host ant specificity for all five European *Phengaris* spp., with each surviving significantly better in the nests of one primary host ant species.

Chemical mimicry can offer an explanation for host ant specificity and how it changes over the course of adoption. Elmes et al. (2002) analysed the chemical signatures of five *Myrmica* spp. and found the cuticular hydrocarbon profile of each to be highly distinctive; maintaining high levels of social exclusion between them. This means a *Phengaris* spp. larva closely mimicking the chemical profile of one *Myrmica* species is likely to be rejected by other *Myrmica* spp., resulting in host-specificity (Thomas et al. 1989). However, the chemical profile of *Phengaris* spp. larvae changes over the course of adoption. Schonrogge et al. (2004) found that newly emerged 4th instar *P. rebeli* larvae have simpler hydrocarbon signatures than that of their host ant, *M. schencki*. It is only after adoption that the larvae gain more complex signatures and begin to mimic their hosts more closely (Schonrogge et al. 2004). Elmes et al. (2002) found that the similarity between *P. rebeli* and *M. schencki* hydrocarbon profiles was much closer when compared again 1 week after adoption. The initial simple chemical profile of *Phengaris* spp. larvae does promote adoption by primary host ant species more than others but it is not very specific at this stage. When developing a more complex chemical profile post-adoption, the larvae may then begin to synthesise more compounds specific to their primary host species, increasing the likelihood of rejection by other *Myrmica* spp. This would explain why despite initially being adopted by any member of the *Myrmica* genus, *Phengaris* spp. larvae usually fail to mature in nests other than those belonging to their primary host (Elmes et al. 2002).

However, this system of extreme host ant specificity has developed since it was first proposed and a more intricate view now accepts that other *Myrmica* spp. may sometimes function as secondary hosts (Pech et al. 2007). A very small percentage of larvae can be supported by *Myrmica* spp. other than their primary host if conditions are very favourable (Schonrogge et al. 2004). For example, around 90 percentage of adult *P. arion* in the UK emerge from *M. sabuleti* nests but around 10 % emerge from nests of the very closely related *Myrmica scabrinodis* (Sielezniew and Stankiewicz-Fiedurek 2008). These secondary host species normally support very few *Phengaris* spp. larvae through to maturity. However, during years when the primary host population experiences severe declines, secondary hosts may be essential for preventing local population extinction of *Phengaris* spp., enabling them to persist until conditions become more favourable (Thomas and Simcox 2005). The fact that *Phengaris* spp. hydrocarbon profiles are initially simple may be an adaptation that allows non-host ants to adopt larvae of *Phengaris* spp., if occasionally required (Schlick-Steiner et al. 2004).

This system seems to provide suitable guidelines for explaining most observed *Phengaris*-*Myrmica* spp. interactions (Barbero et al. 2012). However, more recent data demonstrates that host ant specificity may not be consistent across the European range of *Phengaris* spp. (Barbero et al. 2012). *P. arion* populations exist in many different biotopes across Europe. The composition of *Myrmica* spp. differs drastically between many of these biotopes because *Myrmica* spp. are very sensitive to changes in micro-climate (Pech et al. 2007). Most of the early research on *P. arion* took place in Britain and parts of Western Europe due to interest at the time being focussed on the declining UK population (Casacci et al. 2011). This meant that study sites only looked at a very small part of *P. arion*'s range, with very similar biotopes, in which *M. sabuleti* traditionally dominates (Pech et al. 2007). More recent studies looking at numerous different biotopes over *P. arion*'s range reveal that *P. arion* populations still persist in areas where *M. sabuleti* is scarce or absent. For example *M. sabuleti* is not found in Finland but *P. arion* is still present (Kolev 1998, cited by Pech et al. 2007). Sielezniew et al. (2010) looked at *P. arion* host ant use in five different locations in five different biotopes across Poland. Altogether five *Myrmica* spp. were found to host *P. arion* and at one site it seemed very likely that an alternative primary host was being used. In Gugny NE Poland the parasitisation rate of *Myrmica lobicornis* was significantly higher than that of any other species including *M. sabuleti* (Sielezniew et al. 2010). Other studies have observed similar changes in host ant exploitation for the other European *Phengaris* spp., with *P. alcon* possibly possessing three primary hosts over its range (Elmes et al. 1998). These new observations seem to contradict the findings of Thomas et al. (1989) and place a lot of doubt on the idea that each *Phengaris* species utilises only one primary host ant.

Pech et al. (2007) suggest that these observations could be explained by *Phengaris* spp. being more generalist, with specific associations occasionally being observed due to a limited number of host ant species being present in some areas. However, Sielezniew et al. (2010) stress that recent observations may instead indicate the existence of local specialisations and geographical variation in host ant specificity, rather than *Phengaris* spp. being able to use numerous host ant species in general. This hypothesis still allows *Phengaris* spp. to specialise on different primary hosts, but differs from the species-specificity hypothesis of Thomas et al. (1989) in that these host associations can alter and are strongly dependent on the composition of the *Myrmica* spp. community in a given location (Witek et al. 2008). However, Pech et al. (2007) feel that the local-specialisation hypothesis still fails to explain all observed *Phengaris*-*Myrmica* spp. interactions. For example, at some sites numerous ant species appear to be used as primary hosts at the same time, again giving *Phengaris* spp. the appearance of generalists. In addition, the chemical mimicry exhibited by some *Phengaris* spp. populations suggests that they may possess some adaptations for multi-host use. Schlick-Steiner et al. (2004) found that *P. rebeli* larvae initially possess chemical compounds specific to numerous *Myrmica* spp. and that after adoption they lose the chemical compounds that are not presented by their hosts. There is also some evidence that in non-host colonies the biosynthesis of host ant chemical cues can be halted (Schonrogge et al. 2004). Evidently host ant specialisation in *Phengaris* spp. is much more complex than was once thought as new observations continue to challenge existing hypotheses regarding its specificity.

Range of *P. arion* and its host ant niche

P. arion has a global range that occupies much of the Palearctic with its distribution centred on Central and Eastern Europe. Its range extends in a band that reaches west to France, Norway and the UK and east through to Southern Siberia, Mongolia and China (Wynhoff 1998). Across this large area *P. arion* is restricted to locations that support the co-occurrence of suitable host ant and host plant species (Thomas et al. 2011). *Thymus* spp. can survive in most locations that maintain an early successional stage (Muggleton and Benham 1975) but *Myrmica* spp. have a comparatively narrow niche (Griebeler 2011). This means that the host ant of *P. arion* is more likely to restrict and dictate its fine-scale distribution than its host plant. Research triggered by the decline of *P. arion* in the UK suggested it was restricted to locations that support the species *M. sabuleti* (Thomas 1980). Recent observations indicate that this may not always be the case but the host ant specificity of *P. arion* is an ongoing debate and a reliance on *M. sabuleti* as its primary host seems to explain the species' extinction in the UK (Thomas 1980). *P. arion* conservation attempts based on reviving *M. sabuleti* populations in the UK have also proved successful (Thomas et al. 2009). Therefore it is still useful to understand the characteristics of *M. sabuleti*'s niche for informing where *P. arion* can occur, especially for the reintroduced UK population.

Myrmica spp. occupy very similar ecological niches but differ in their physiological responses to temperature (Elmes and Wardlaw 1982a). *M. sabuleti* is a thermophilous ant, which develops and works most quickly in warm environments when its brood chambers are heated to around 21 °C (Elmes and Wardlaw 1982b). If this temperature drops by even one degree this may be enough for less thermophilous *Myrmica* spp. such as *M. scabrinodis*, to outcompete and completely replace *M. sabuleti* in a given area (Elmes and Wardlaw 1982a). Ground temperature correlates closely with insolation and this is affected by several factors including latitude, local aspect and sward structure. Varying combinations of these factors can produce the optimal soil temperature required for *M. sabuleti*, which causes its niche to vary in different climes (Elmes and Wardlaw 1982b). However, as temperatures become progressively extreme towards the borders of its range its niche becomes increasingly narrow (Thomas et al. 1998). Eventually no local change in micro-climate can alter regional temperature enough to support *M. sabuleti*, marking the edge of its global range as well as *P. arion*'s (Thomas and Simcox 2005). Near its northern latitudinal limits in the UK, *M. sabuleti* is confined to warm south facing slopes where swards are maintained at heights of less than around 3 cm. These conditions enable as much solar radiation to heat the ground as possible, enabling the thermophilous ant to survive in cold climes (Thomas and Simcox 2005). Further south the warmer temperatures mean that *M. sabuleti* can be found on flat land as well as south-facing slopes and *M. sabuleti* can breed amongst slightly taller 5 cm swards, which cool the ground below (Thomas and Simcox 2005). Finally, in the south of France the highest densities of *M. sabuleti* are found on flat ground amongst very tall swards reaching 30 cm in height. *M. sabuleti* is not found on south-facing slopes as temperatures are too hot and an even more thermophilous ant such as *M. schencki* usually dominates (Thomas and Simcox 2005).

The way in which sward structure can locally alter a site's micro-climate makes it an extremely important factor in controlling the distribution of *P. arion* (Barnett and Warren 1995). The long-term decline and eventual extinction of *P. arion* in the UK is thought to be linked to a decrease in closely cropped grasslands (Thomas 1980). Site destruction and improvement for agriculture using pesticides may account for the disappearance of around half of the *P. arion* colonies in the UK (Barnett and Warren 1995). The rest are thought to have been affected by land abandonment and the relaxation of grazing, which has progressed quickly since the 1950s (Barnett and Warren 1995). This will have allowed much of the remaining grassland in the UK to grow rapidly above 3 cm and allow *M. scabrinodis* to outcompete and replace *M. sabuleti* (Thomas 1980). This problem was exacerbated by an outbreak of myxomatosis, which caused rabbit populations to plummet and even less grassland to be grazed (Barnett and Warren 1995). With *P. arion*'s primary host ant becoming increasingly scarce it is thought that the UK population could no longer be supported, leading to its extinction in 1979 (Thomas et al. 2009).

Implications for conservation in the UK

The complex lifecycle of *P. arion* and its dependency on two specific larval resources causes high juvenile mortality rates and results in its populations experiencing substantial bottlenecks every generation (Ugelvig et al. 2011a). Many eggs are laid outside of host ant territories, larvae are adopted by non-host ants and intense scramble competition within *Myrmica* spp. nests can lead to the early exhaustion of the host ant brood and starvation (Thomas and Elmes 2001). This presents considerable problems for the conservation of the species as in addition to needing to maintain very specific conditions for an extremely narrow niche (Thomas et al. 1989), a small effective population size limits population growth, whilst also reducing the genetic variability and evolutionary potential of the species to cope with environmental changes (Andersen et al. 2014).

However, despite this, the reintroduction of *P. arion* to the UK is one of the major success stories in insect conservation, with UK sites now hosting the highest known densities of *P. arion* in the world (Andersen et al. 2014). Since its re-introduction from Swedish stock populations in Oland in 1983 *P. arion* has been recorded on approximately 40 sites in the UK, although some of these are stepping stone sites which can disappear and then be recolonised in line with the success of larger core populations. Short and long term projects are also in place to restore habitat to around a further 100 sites (D. Simcox 2015 pers. comm.).

Habitat management has been directed towards creating suitable conditions for *M. sabuleti,* the specific host ant of *P. arion* in the UK, maintaining the short turf that this thermophilous ant requires to encourage foraging. Conserving this habitat in turn provides suitable conditions for *Thymus* spp. to grow, free from the threat of succession. In this way, scrub clearance and the reintroduction of grazing schemes have been used to create suitable habitat for *M. sabuleti*, which in turn supports the co-occurrence of specific host plants and the growth of large populations of *P. arion* (R. Jones 2015 pers. comm.). No studied site in Europe has near as high a co-occurrence of food plant and *M. sabuleti* ranges than restored UK sites (Andersen et al. 2014), highlighting that this is likely to be a key factor in the success of the UK reintroduction programme.

The maintenance of stable host ant populations is clearly essential to the conservation of *P. arion* and other *Phengaris* spp. Undertaking regular ant surveys, to allow for reactive management dependent on ant density and movement, has therefore proven very important for ensuring the effective exploitation of *M. sabuleti* colonies and the sustainable growth of *P. arion* populations (R. Jones 2015 pers. comm.) The potential for overexploitation of ant colonies has crucial implications when creating habitats for *Phengaris* spp. Clarke et al. (1998) modelled the interactions between *P. rebeli* and its larval resources to assess the effect of host plant density and spatial distribution on population dynamics. The model predicts that optimum host plant density is reached at around 1500 per hectare with plants distributed according to natural clumping. Beyond this adding extra host plants, especially within gaps in the site, is actually predicted to reduce host ant populations and that of the *Phengaris* spp. they support. It appears that *Myrmica* spp. refuges, free from the effects of *Phengaris* spp. parasitisation, are essential for maintaining stable host ant populations. This is why the spatial distribution of resources within a site, not just overall density, appears to be so important as this can alter the size of ant refuges (Clarke et al. 1997). Nowicki et al. (2013) found similar results for *P. nausithous*, which shows a preference for habitat edges opposed to interiors. They propose that this may be due to the areas surrounding the habitat acting as a refuge for *Myrmica* spp., potentially causing there to be a higher abundance of healthy host ant colonies at the habitat edge.

Random oviposition on suitable host plants and the apparent absence of the use of host ant cues in the ovipositional behaviour of *P. arion* (Thomas and Elmes 2001) exacerbates the problem of trying to ensure sustainable exploitation of *M. sabuleti* nests. Pheromones which deter oviposition could potentially help prevent overexploitation of *Myrmica* spp. colonies but only limited evidence of this hypothetical pheromone has been found for *P. teleius*. Furthermore, ovipositional behaviour of *P. arion* does not suggest its use (Sielezniew and Stankiewicz-Fiedurek 2013), reinforcing the need for regular monitoring of *Myrmica* spp. colonies and reactive management in the conservation of *P. arion* (R. Jones 2015 pers. comm.).

The importance of landscape scale conservation has also been recognised for the maintenance of *P. arion* in the UK as it enables sites to be recolonised if occasional management errors occur (D. Simcox 2015 pers. comm.). *Phengaris* spp. were originally considered to be extremely sedentary but there is now increasing evidence that they can cover distances of several kilometres between suitable habitat patches (Radchuk et al. 2012). A patchy stepping stone network linking reserves can therefore help maintain populations and bolster against the local extinction of these vulnerable specialists (Jansen et al. 2012). Furthermore, interconnecting populations is important for maintaining genetic diversity of these species, countering the effects of genetic drift on a very small effective population size (Ugelvig et al. 2011a). The natural recolonization of 23 UK sites in the Polden Hills by *P. arion* after reintroduction, which spread by stepping stone occupation of neighbouring habitat patches, highlights how creating suitable nearby habitat is key for encouraging the dispersal and spread of *P. arion*. (Thomas et al. 2009).

A final factor that should be considered when trying to protect populations of *P. arion* is the potential threat posed by parasitoid wasps. Fortunately, observations of *I. eumerus* and its host *P. rebeli* suggest that the wasp only has a small impact on its host population, largely due to the wasp being long lived and having a slower reproductive rate than the butterfly (Hochberg et al. 1998). However, where the parasitoid does occur 6–23 % of the population can be parasitised. This could still cause serious issues for new, small *Phengaris* spp. populations struggling to get established. Unfortunately parasitisation of *P. arion* is difficult to prevent as habitat generated to support a *Phengaris* spp. will subsequently support its parasitoid (Hochberg et al. 1998). The best course of action may well be to continue promoting the growth of large populations of *P. arion* and interlinking sites so that recolonization can take place in case any areas are overexploited by parasitoids and local extinction occurs.

Radchuk et al. (2012) used a spatially explicit model to look at how four equal cost management options would affect *P. alcon* populations: increasing habitat area, increasing habitat quality, creating stepping stone sites and translocations. Overall the most promising option appears to be the enlargement and restoration of habitat patches followed either by improving habitat quality or creating a network of stepping stone sites. Restoring and enlarging habitat patches is the most cost effective method of conservation as buying up additional stepping stone land is comparatively expensive and, for the same cost, increasing habitat quality does not increase a habitat's carrying capacity as much as increasing the habitat's area. However, the model notes that the best option for promoting long term persistence, if available, would be to create a large area of high quality habitat placed within an area of stepping stone patches, allowing at least limited connectivity to other sites (Radchuk et al. 2012).

The models predictions of optimal management strategies for *Phengaris* spp. fall nicely in line with *P. arion* conservation efforts in the UK. The UK now possesses a growing network of interlinked *P. arion* sites of high habitat quality, supporting the co-occurrence of their host plant and host ant (D. Simcox 2015 pers. comm.; R. Jones 2015 pers. comm.). Despite an extremely complex lifecycle and its dependency on specific larval resources our increased understanding of *P. arion* ecology is enabling the creation and restoration of large areas of suitable habitat, promoting population growth.

Conservation across Europe and climate change

Across Europe the regional climatic differences will necessitate different management programmes from those used in the UK. Different sward structures will have to be maintained to create the specific micro-climate required by the host ants of *P. arion* (Thomas and Simcox 2005). Furthermore, the potential for *P. arion* to make use of different or numerous primary host ants across the continent (Sielezniew et al. 2010) will necessitate sward structures to be maintained at suitable levels for the specific host *Myrmica* spp. in any given region (Thomas and Simcox 2005).

Another important question that has to be answered is how much *P. arion* is likely to be able to cope and adapt to changing climatic conditions and how the conservation of the species can be ensured into the future. This will again likely differ across Europe as populations of *P. arion* specialising on only one host ant species may be more restricted than those capable of parasitising many (Dennis et al. 2011). Therefore, the pattern and regional distribution of specialist and potentially more generalist populations of *P. arion* must be deduced for conservation measures to be successfully implemented across the continent. This will necessitate further research into regional *Phengaris-Myrmica* spp. associations.

Across Europe, differences in historical climate patterns after the last glacial maxima will likely have caused variations in range expansions, contractions and the degree of isolation of *P. arion* populations (Dennis 1977). This could have in turn caused the degree of host specialisation to differ between regions (Dennis et al. 2011), with the maintenance of multiple host ant use amongst populations of *P. arion* potentially being possible so long as they continued to co-exist with diverse *Myrmica* spp. communities. The UK population of *P. arion* is thought to have been isolated from the continent by around 7.5 ka BP. due to vegetation succession and forest closure (Dennis 1993). During the Sub Atlantic period of the Holocene a shift in the UK's climate towards cooler and damper summers may then have caused contraction of the range of the now isolated UK *P. arion* population (Dennis, 1977). Isolation and climatic downturn likely lead to *P. arion* adapting to the new climate regime and specialising on the now more limited resource base (Dennis et al. 2011), dominated by the host ant *M. sabuleti* (Pech et al. 2007). However, populations on the continent may have benefitted from a warmer, dryer climate, and potentially underwent less severe range contractions and isolations (Dennis 1977). This may explain why host ant use and the niche of *P. arion* appears to be less restricted on the continent than in the UK (Sielezniew et al. 2010; Thomas et al. 1998).

The limited host ant use of *P. arion* in the UK presents further problems in light of projected climate change as *P. arion* is already an extremely specialised species with a very narrow niche (Thomas et al. 1989). Despite this, there may be cause to be cautiously optimistic as the UK population of *P. arion* has maintained a similar level of genetic diversity to its source populations on the continent, suggesting that they may have equal evolutionary potential to cope with climate change (Andersen et al. 2014). However, although the UK population has maintained the same level of genetic variation as continental populations, this is likely due to the strange population structure of *Phengaris* spp., rather than it being an indication that *P. arion* is well suited to relocating and thriving in new climates. This is reinforced by the fact that after just 19 generations the UK population has already become genetically differentiated, having several private alleles not found in the Swedish source populations (Andersen et al. 2014). It might appear that *P. arion* is capable of rapidly adapting to local climatic pressures, unfortunately it is more likely that the tiny effective population size of *P. arion* causes genetic drift to make populations rapidly diverge after isolation. This is probably why the bottleneck associated with translocating *P. arion* to the UK did little to reduce genetic diversity as all *P. arion* populations go through bottlenecks each generation anyway, causing a similar but low level of genetic diversity across sites (Ugelvig et al. 2011a). Kajzer-Bonk et al. (2013) found that short lived natural catastrophes also appear to have negligible impact on *Phengaris* spp. when investigating how flooding affected *P. nausithous* and *P. teleius* populations. Therefore, *Phengaris* spp. are apparently somewhat resistant to the effects of genetic erosion caused by frequent bottlenecks but the strong influence of genetic drift may give local adaptations relatively little chance to evolve, meaning that *P. arion* is unlikely to be able to quickly adapt to new climates (Ugelvig et al. 2011a). In the future translocations may help to conserve *P. arion* populations in the UK as climate change causes the distribution of suitable habitat patches to shift. Natural dispersal of *P. arion* may even allow some degree of habitat tracking as the climate changes, however, the dispersal of *P. arion* in this way would likely take an extremely long time as the reintroduced UK population took 14 years to travel naturally to a site 4.4 km from its source (Thomas et al. 2009). Conservation efforts should therefore look at maintaining the suitability of sites that currently support *P. arion*, whilst bearing in mind that translocations may be used if needed.

One factor that may benefit *P. arion* over *Phengaris* spp. that utilise cuckoo behaviour is that generally the more loosely integrated larvae of *P. arion* survive better in non-host *Myrmica* spp. nests (Thomas and Elmes 1998). Furthermore, in extreme years *P. arion* has been seen to use and survive on alternative hosts such as *O. vulgare* and *M. scabrinodis* (Sielezniew and Stankiewicz-Fiedurek 2008). Nevertheless, it is very optimistic to hope that *P. arion* will be able to change its hosts. Even though secondary hosts may help buffer populations against extinction, after more than 1 or 2 years on any site where its food plant does not coincide with its primary host ant, *P. arion* will not survive (Thomas and Elmes 1998). Indeed maintaining non-host populations of *Myrmica* spp. with suitable host plants was partially responsible for the failed conservation of the original UK population of *P. arion* (Elmes and Thomas 1992). Instead it is likely that in a warming climate the management of current *P. arion* sites in the UK will have to be altered to maintain the precise temperature and microclimatic niche of *M. sabuleti*. As regional temperatures rise the effect of vegetation shading will likely be reduced and *M. sabuleti* populations will be able to occupy slightly taller turf. Grazing regimes on current sites must then alter to maintain swards at this slightly taller optimum height so that *M. sabuleti* is not outcompeted by even more thermophilous ants (Thomas and Simcox 2005). Thomas et al. (2009) found evidence that *M. sabuleti* populations in the UK may already be beginning to occupy areas with slightly taller swards, potentially as a result of a warming climate. Although *P. arion* unlikely has much potential to adapt to an altering climate, changing management regimes may enable current *P. arion* habitats to remain suitable for *M. sabuleti* into the future and for *P. arion* to continue being supported in the UK for years to come.

Conclusions

Since 1972, when research into the ecology of *P. arion* was triggered by the decline of the UK population, a huge amount has been learnt about the complex life cycle and associated requirements of this fascinating butterfly. Key advances have been made in many areas of our understanding regarding *P. arion* including: the nature of its ovipositional cues, its host ant specificity and the characteristics of its host ant niche. Evidence suggests that *P. arion* primarily uses host plant bud phenology to determine site of oviposition (Thomas and Elmes 2001) and that in the UK *P. arion* is dependent on one primary host ant species, *M. sabuleti*, which requires closely cropped grasslands to survive (Thomas et al. 1989). These findings have enabled the successful reintroduction of *P. arion* into the UK by informing the maintenance of closely cropped grasslands suitable for its host *Myrmica* species (Thomas et al. 2009). However, this research has also produced new questions and revealed high degrees of complexity which were not previously considered.

For example, it is unclear how the host specificity of *P. arion* changes over its European range. Future analysis comparing the chemical profiles of *P. arion* populations with co-occurring *Myrmica* spp. could help resolve whether or not *P. arion* mimics different *Myrmica* spp. in different locations. This research could also reveal the degree to which *P. arion* larvae synthesise novel compounds or simply acquire those of their host colony in order to complete their gestalt odours. Another unanswered question that might benefit from further examination is how the near identical acoustic signals of predatory and cuckoo *Phengaris* spp. produce different responses from their host ants. It may be that some aspect of *Phengaris* spp. stridulations is being overlooked or that by using stridulations in combination with different signals, or in different contexts, their effect is altered. Finally, although ant-related oviposition seems unlikely, existing studies have not definitively demonstrated its absence. Future research aimed at controlling for other potential ovipositional cues might be able to show the effect of host ant distribution on the oviposition of *P. arion* more clearly.

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