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Escape from natural enemies during climate-driven range expansion: a case study

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Abstract. 1. A major, and largely unexplored, uncertainty in projecting the impact of climate change on biodiversity is the consequence of altered interspecific interactions, for example between parasitoids and their hosts. The present study investigated parasitism in the Brown Argus butterfly, *Aricia agestis*; a species that has expanded northward in Britain during the last 30 years in association with climate warming.

2. *Aricia agestis* larvae suffered lower mortality from parasitoids in newly colonised areas compared with long-established populations. This result was consistent over four consecutive generations (2 years) when comparing one population of each type, and also when several populations within the historical and recently colonised range of the species were compared within a single year. Thus, *A. agestis* appears to be partially escaping from parasitism as it expands northwards.

3. Reduced parasitism occurred despite the fact that several of the parasitoid species associated with *A. agestis* were already present in the newly colonised areas, supported predominantly by an alternative host species, the Common Blue butterfly, *Polyommatus icarus*.

4. As the species expand their distributions into areas of increased climatic suitability, invasion fronts may escape from natural enemies, enhancing rates of range expansion. The results suggest that the decoupling of interspecific interactions may allow some species to exploit a wider range of environments and to do so more rapidly than previously thought possible.

Key words. *Aricia agestis*, butterfly, climate change, enemy escape, parasitoids, range expansion.

Introduction

There is increasing evidence that climate change is leading to shifts in the distribution of many species (Thomas & Lennon, 1999; Parmesan & Yohe, 2003; Root *et al.*, 2003). A frequent approach for predicting the consequences of these changes for biodiversity is to project range changes into the future using bioclimate/distribution/niche models (e.g. Peterson *et al.*, 2004; Thomas *et al.*, 2004). This approach assumes that species' future ranges can be projected as a function of climate, given accurate scenarios of future climate change. However, other factors including habitat availability and species interactions are known to play important roles in determining species abundances and distributions (Davis *et al.*, 1998; Hill *et al.*, 1999) and may affect the extent to which the distributions of species track shifting climate envelopes (Lawton, 2000).

Research on biological invasions has emphasised the importance of multi-species interactions for the dynamics of range boundaries (Gaston, 2003). Invading species may be attacked by fewer enemies, and suffer reduced levels of mortality in newly colonised areas, increasing the rate of expansion (see Colautti *et al.*, 2004; Liu & Stiling, 2006 for a review). Specialist enemies may be absent at the expanding margin of their prey or host's range, and generalist enemies may not search in appropriate locations to find the invader. These possibilities, however,

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have not been explored in relation to climate change, and the outcome could be quite different in this context. The biological invasions literature has largely considered species that have been transported long distances by humans, and that have left some or all of their natural enemies behind (Clay, 2003; Mitchell & Power, 2003; Torchin *et al.*, 2003; Gröbler & Lewis, in press). Such invasive species will often be taxonomically or biologically distant from native species in the area under invasion, so natural enemies may not switch quickly to the invading host or prey. In contrast, natural enemies might be able to track species expanding their distributions in response to climate change much more effectively, given that the initial distribution change does not usually involve long-distance movement away from the long-standing geographic range, and that related species harbouring shared natural enemies may already occur in the regions of expansion.

The present study tests the hypothesis that a species that has moved northwards as the climate has warmed has escaped from its natural enemies.

Materials and methods

The study system

The study organisms were the Brown Argus butterfly [*Aricia agestis* (Denis and Schiffermüller)] and its parasitoids. *Aricia agestis* has expanded its distribution northwards in Britain, moving at about 10 km per year since the early 1990s (Fig. 1a). This expansion appears to have been triggered by the increases in temperature experienced in recent decades (Asher *et al.*, 2001; Warren *et al.*, 2001; Fox *et al.*, 2006) and also by a shift in habitat and host plant used by the butterfly during the expansion (Thomas *et al.*, 2001). *Aricia agestis* has spread away from calcareous grassland habitats (where its main host plant is *Helianthemum nummularium* Linnaeus) into other types of grassland, where its larvae feed on Geraniaceae species (mainly *Geranium molle* Linnaeus and *Erodium cicutarium* Linnaeus). This habitat change has been achieved because new expanding populations are dominated by a form of the butterfly that prefers to lay eggs on *G. molle* (Thomas *et al.*, 2001) irrespective of the natural host plant existing in the area. However, genetic variation for host plant selection was already present in *A. agestis* populations in Britain previous to the expansion. In some southern populations caterpillars were feeding only on Geraniaceae species, and caterpillars from all populations studied, including those that naturally feed on *Helianthemum*, exhibit faster larval growth when fed *Geranium* than *Helianthemum* species in captivity, at a given temperature (Bodsworth, 2002). Thus, the expansion must have been triggered by other factors. Trends in the abundance of *A. agestis* in several populations across Britain (U.K. Butterfly Monitoring Scheme, http://www.ukbms.org/) showed that population increases are positively correlated with summer temperature and negatively correlated with rainfall (Asher *et al.*, 2001). In addition, *Helianthemum* plants often grow on sheltered and southerly facing hillsides, and these habitats have been demonstrated to be warmer (i.e. they deliver more cumulative degrees-days $>10\,^{\circ}\mathrm{C}$, resulting in faster larval growth) than most *Geranium*-containing habitats (Bodsworth, 2002). For this reason, most northern habitats containing Geraniaceae host plants were probably too cold for the development of caterpillars during the 1960s and 1970s, but warm enough in the 1980s and 1990s. Thus, climate warming is likely to be responsible for the northward expansion of *A. agestis* in Britain by allowing a rapid development of a wider diet and range of available habitats at the range limit of the species. This idea of climate-driven expansion is also supported by the fact that the species has also colonised several *Helianthemum* areas further north (see Appendix).

By expanding to new areas the butterfly might have left its parasitoids behind. Additionally, the shift onto a new host plant may have also affected the ability of parasitoids to find *A. agestis* caterpillars in the newly colonised areas. Before this study, little was known about the parasitoids attacking the caterpillars of *A. agestis* in Britain. Five other closely related lycaenid butterflies occur in low plant communities in Britain and share parasitoid species with *A. agestis* (Shaw *et al.*, 2008). *Polyommatus icarus* (Rottemburg) is the most abundant and widespread species of lycaenid in Britain. It occurs in almost all areas where *A. agestis* is present and its distribution extends much further north. In Britain, *P. icarus* and *A. agestis* share at least four parasitoid species, all of them specialised on lycaenid butterflies [*Cotesia saltatoria* (Balevski), *Aleiodes bicolor* (Spinola), *Hyposoter notatus* (Gravenhorst) and *Aplomyia confines* (Fallén); Shaw *et al.*, 2008]. The first three of these have also been reared in Britain from *Aricia artaxerxes* (Fabricius) (Shaw, 1996, 2007), which has an entirely more northerly British range than *A. agestis*.

Parasitoid species attacking Aricia agestis *in Britain*

In three consecutive years (2002–2004), a total of 16 sites across the range of *A. agestis* were visited (Fig. 1c, Appendix) to investigate the parasitoid complex attacking the larval stage. Sites were classified into two categories based on the time since colonisation by the butterfly: eight sites within the established part of the range (butterfly recorded since the early 1970s, but probably in most cases present for centuries) and eight newly colonised sites (colonised after 1993). Time of colonisation was established using distribution data (Asher *et al.*, 2001) and information provided by local experts. These areas also differ in the natural host plant used by the butterfly (see Appendix).

Wild caterpillars were collected from the field (second and third instar out of the four instars passed through by this species) and reared in the laboratory until they produced either parasitoids or adult butterflies. Caterpillars were collected in spring, prior to the first adult emergence of butterflies in early summer (hereafter *first generation*) and then again in mid summer, prior to the second adult emergence in late summer (*second generation*). During the second generation in 2003, we also carried out an experimental exposure of caterpillars to parasitoids in 10 of the 16 areas. In each of these areas, one egg (5–7 days after having been laid in the laboratory by females collected from the field in the previous generation) was transferred on to each of 100 host plants occurring naturally in each area (*Helianthemum nummularium* or *Geranium molle* dependent on area). The resulting caterpillars were collected after 14 days, by which time

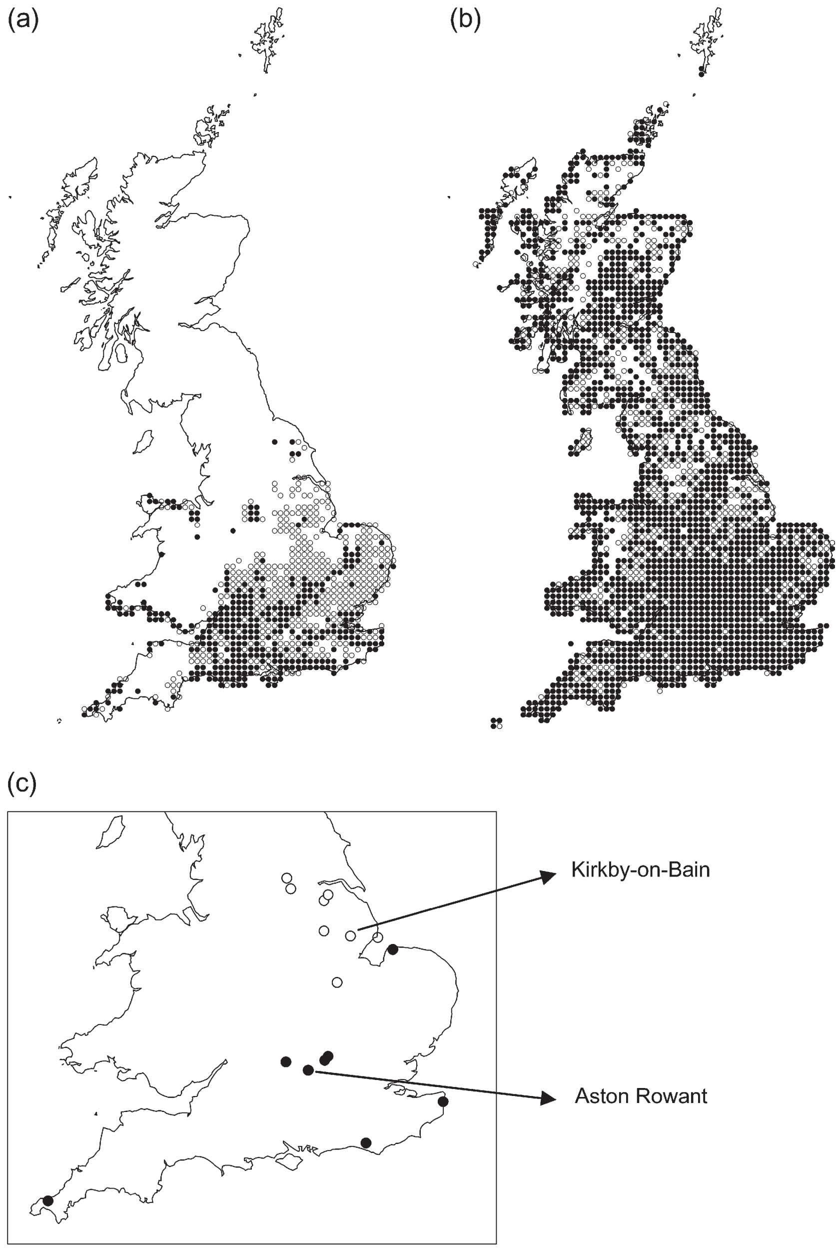

Fig. 1. Distribution of (a) Brown Argus (*Aricia agestis*) and (b) Common Blue (*Polyommatus icarus*) in Britain. Black circles show that the species was present in 1970–1982; open circles show newly colonised areas (1995–1999 records, not present in 1970–1982). Circles represent 10 km grid cells (maps modified from Asher *et al.*, 2001). (c) Sampling locations (black, long-established populations of *A. agestis*; open, newly colonised populations).

they were probably in their second instar, together with the wild caterpillars found in the same population. Experimental caterpillars provided approximately 70% and 80% of the collected caterpillars during that generation, from the old and the new part of the range respectively.

Rarefaction (Simberloff, 1972) was used to compare the number of parasitoid species attacking *A. agestis* caterpillars in the new vs. the long-established part of the species range. This approach controls for differences in sampling effort between samples by comparing parasitoid species richness at a standardised sample size (in this case, the number of parasitoid individuals in the smallest sample).

The mortality attributable to a particular parasitoid species in the established and in the new part of the range was calculated as the percentage of caterpillars parasitised by that parasitoid species, pooling data from all populations within each range category, given the sample sizes available in each population (see below and Discussion).

Parasitism rate in areas within the new vs. established part of the range

Measuring parasitoid attack in the field proved to be difficult, mainly because of the difficulty of finding sufficient caterpillars. As a result, sample sizes for some sites, generations and years were too small to test statistically for differences in parasitism rate using all sites. However, during the first generation of the butterfly in 2004 enough wild caterpillars were collected from six sites (three within the new and three within the established part of the range) to test for differences in observed parasitism rate between new and long-established populations. Observed parasitism rate was calculated as the number of parasitised caterpillars divided by the total number of caterpillars collected from each population, and expressed as a percentage. Differences in observed parasitism rate between new and long-established populations and between populations differing in terms of the host plant used by the caterpillars were analysed using Mann–Whitney tests.

Temporal variability in parasitism rate: a new vs. an old population

Inter-generational and inter-annual variation in observed parasitism rate were measured in two of the above-mentioned areas, one site within the established part of the range (Aston Rowant, Fig. 1c) and the other within the new part of the range (Kirkby-on-Bain, Fig.1c). At these two sites, caterpillars were collected in sufficient numbers in four consecutive generations (second 2002, first and second 2003 and first 2004) to carry out analyses. Observed parasitism rate per generation was calculated as described above.

During the second generation in 2003, we also carried out an experimental exposure of caterpillars to parasitoids in these two areas as described above. No differences were found in observed parasitism rates between wild and experimental caterpillars from the same area, so data were pooled for analysis [Aston Rowant: 78% parasitism for experimental ($n = 18$) and 67% parasitism for wild caterpillars ($n = 21$), $P = 0.497$; Kirkby-on-Bain: 31% parasitism for experimental ($n = 29$) and 33% parasitism for wild caterpillars ($n = 9$), $P = 1.000$].

Parasitism rate of Aricia agestis *vs. a long established host* (Polyommatus icarus)

To compare levels of observed parasitism rate of the new host (*A. agestis*) with a long-established alternative host in the same locality, caterpillars of the Common Blue butterfly (*P. icarus*) were also collected at Kirkby-on-Bain and Aston Rowant during the four consecutive generations mentioned above. *Polyommatus icarus* is the only butterfly species belonging to the same subfamily, Polyommatinae, in the areas newly colonised by *A. agestis*. This species also has two generations per year that overlap with those of *A. agestis*. As mentioned before, *P. icarus* shares at least four of its most important parasitoid species with *A. agestis* (Shaw *et al.*, 2008), and it has been present in the two areas since long before the 1970s (Fig. 1b). Differences in observed parasitism rate (averaged over the four generations) between the two species were analysed using Mann–Whitney tests.

Results

Parasitoid species attacking Aricia agestis *in Britain*

A total of 312 and 114 *A. agestis* caterpillars were collected from sites within the new and the established part of the butterfly range respectively. Seventy-eight (25%) and 61 (54%) of these caterpillars died from parasitism, respectively, indicating a higher level of parasitism in the established part of the range ($\chi^2 = 30.87$, $P < 0.001$).

Table 1 shows the complex of parasitoid species attacking the larval stage of *A. agestis* in new and established parts of its range. Caterpillars were attacked by a total of six species of parasitoids, six species in the established and five species in the new part of the range (4.8 ± 0.1 species of parasitoid in the new part of the range based on expected number of parasitoid species in a sample of 61 individuals using rarefaction methods). Although the same parasitoid species were found in both parts of the range, the percentage of the mortality attributable to a particular parasitoid species differed between the two parts of the range (Table 1). *Hyposoter notatus* was the species responsible for most parasitism in the established part of the range, while *Cotesia astrarches* was the most frequent parasitoid in newly colonised areas.

Parasitism rate in new vs. long-established populations

Observed parasitism rate for *A. agestis* caterpillars varied significantly between the established and new parts of the range for the subset of six sites sampled during the first generation in 2004 (Mann–Whitney, $Z = -1.96$, $P < 0.05$). Parasitism attack was lower in caterpillars collected from newly colonised areas (Fig. 2a). No significant differences in observed parasitism rates

Table 1. Parasitoid species reared from *Aricia agestis* caterpillars from areas within the long-established and the new parts of the range. Numbers represent percentage of parasitism by different parasitoid species.

Parasitoid species	Established areas	New areas	Likelihood ratio	*P**
Cotesia astrarches (Marshall)	9.9	57.7	37.230	<0.001
Cotesia saltatoria (Balevski)	13.1	32.0	7.109	0.010
Hyposoter notatus (Gravenhorst)	67.2	6.4	62.156	<0.001
Aleiodes bicolor (Spinola)	4.9	2.6	0.542	0.654
Anisobas cingulatellus (Horstmann) (= *cingulatorius* (Gravenhorst))	1.6	1.3	0.031	1.000
Aplomya confinis (Fallén)	3.3	0.0	3.332	0.191

*Fisher's exact test.

were found between populations using different host plants (Fig. 2b, Mann–Witney, $Z = -0.22$, $P = 0.827$).

Temporal variability in parasitism rate: new vs. long-established populations

Figure 3 shows observed parasitism rate of *A. agestis* caterpillars in four generations over 3 years, at Aston Rowant and Kirkby-on-Bain. Observed parasitism rate did not differ between generation within populations (Aston Rowant: $\chi^2 = 3.06$, $P = 0.383$ and Kirkby-on-Bain: $\chi^2 = 2.66$, $P = 0.447$). However, observed parasitism rate was always higher in the long-established Aston Rowant population than in Kirkby-on-Bain, where colonisation was recent (mean ± SE: 75.0 ± 6.9 Aston Rowant and 33.6 ± 5.4 Kirkby-on-Bain; Mann–Whitney, $Z = -2.31$, $P < 0.05$).

Parasitism rate of Aricia agestis *vs. a long established host* (Polyommatus icarus)

Sixty-two *P. icarus* caterpillars from Kirkby-on-Bain and 23 caterpillars from Aston Rowant were collected. Observed parasitism rate differed between the two butterfly species in the newly colonised area at Kirkby-on-Bain (Fig. 4, Mann–Whitney, $Z = -2.31$, $P < 0.05$); the small sample size did not allow us to test for differences between species in the long-established population at Aston Rowant (only 23 caterpillars of *P. icarus* were collected). Observed parasitism rate for *P. icarus* in the newly colonised area was also as high as that observed for *A. agestis* in the long-established population (mean ± SE: 75.0 ± 6.9 *A. agestis* in Aston Rowant and 68.0 ± 8.0 *P. icarus* in Kirkby-on-Bain; $P = 0.486$).

Figure 5 shows the complex of parasitoid species attacking the larval stage of *A. agestis* and *P. icarus* in Aston Rowant (long established) and Kirkby-on-Bain (newly colonised) populations. *Hyposoter notatus* was the species responsible for most parasitism of *A. agestis* in Aston Rowant, but it contributed little to parasitism at Kirkby-on-Bain, where *C. astrarches* was the main parasitoid. In contrast, *P. icarus* experienced a high rate of parasitoid attack by *H. notatus* at Kirkby-on-Bain.

Discussion

Invading insects, and those that are expanding as a result of climate change, may be attacked by fewer parasitoid species and suffer reduced levels of parasitism in newly colonised areas (Cornell & Hawkins, 1993; Schönrogge *et al.*, 1995, 1998). The results of the present study showed that similar numbers of parasitoid species were attacking *A. agestis* in newly (five species) and long-established (six species) populations. This is probably because *A. agestis* parasitoids are not single-host specialists and most of the parasitoid species already occurred far to the north of the distribution of the butterfly, using alternative hosts such as *P. icarus* or *A. artaxerxes* (Shaw, 1996, 2007, 2008). Host recruitment by relatively specialised insect parasitoids seems common when exotic invaders move to an area that contains native congeners (Keane & Crawley, 2002).

Despite the similar species richness of parasitoids in the new part of the range, *A. agestis* caterpillars nonetheless suffered lower overall parasitism rates compared with caterpillars in the long-established part of the range. They also suffered lower parasitism than did caterpillars of *P. icarus*, a host species that has been long established in the same northern localities that *A. agestis* has recently colonised, and also long-established populations of *A. artaxerxes* in more northern sites (67% parasitism was recorded by Shaw, 1996). This suggests that *A. agestis* has partially escaped from its enemies during its northwards expansion in Britain, and this is not a result of latitudinal patterns in parasitism rates.

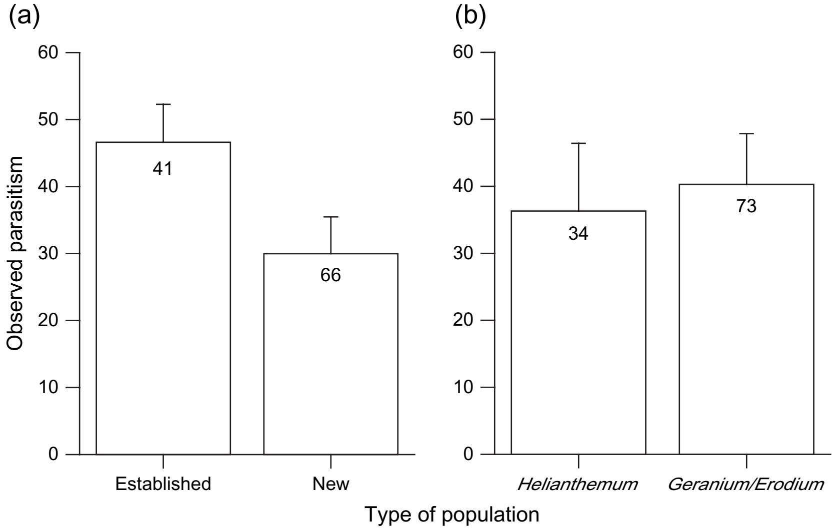

Fig. 2. Observed parasitism (%) of *Aricia agestis* caterpillars (i.e. sum of parasitism by all parasitoid species) during the first generation in 2004: (a) populations that differ in the position within the butterfly range (established vs. new parts of the range), and (b) populations that differ in the host plant used by the butterfly (*Helianthemum* vs. *Geranium/Erodium*). Values are mean + SE and numbers within bars show sample sizes (numbers of caterpillars collected).

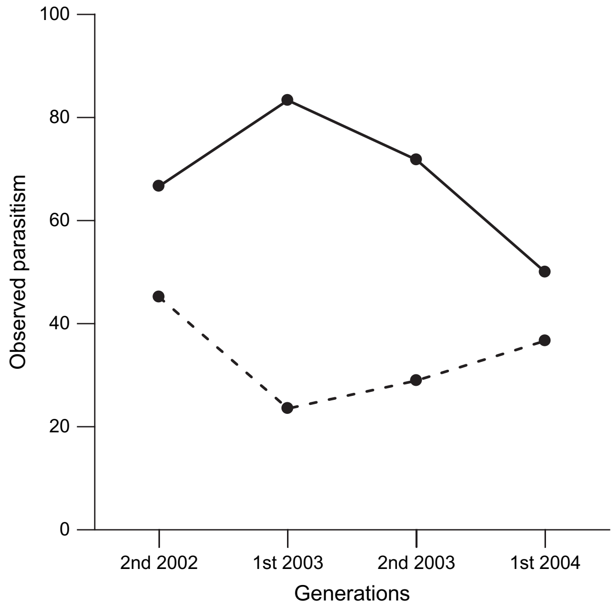

Fig. 3. Observed parasitism (%) of *Aricia agestis* caterpillars, in four consecutive generations, at one site within the established part of the range (Aston Rowant, solid line) and at one newly colonised site (Kirkby-on-Bain, dashed line).

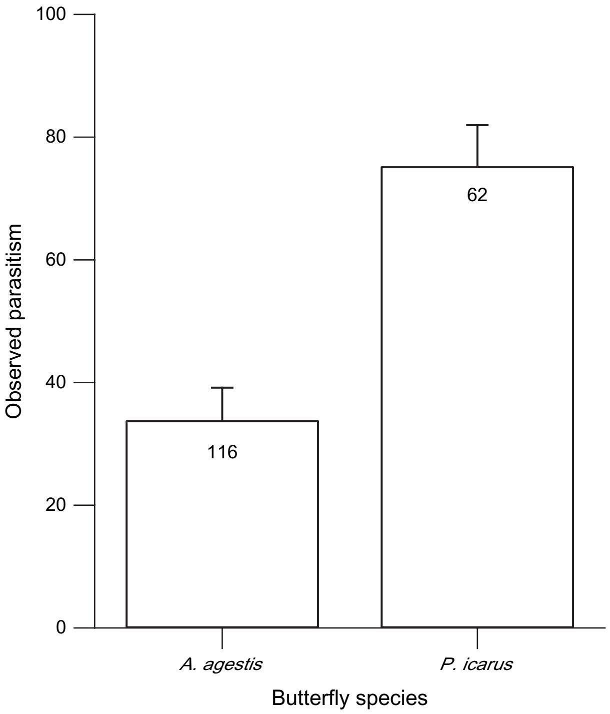

Fig. 4. Observed parasitism (%) of *Aricia agestis* and *Polyommatus icarus* caterpillars at Kirkby-on-Bain (colonised by *A. agestis* in 1995; *P. icarus* present since long before 1970). Values are mean + SE (over four consecutive generations) and numbers within bars show sample sizes (numbers of caterpillars collected).

Several mechanisms may be involved in this escape from enemies, and different mechanisms may be relevant for different species of parasitoids.

1 Enemies are not present in some of the newly colonised sites, so two successful migrations (host and parasitoid) are required. Most parasitoids attacking *A. agestis* in the newly colonised populations were likely to be present there before the arrival of the butterfly, using *P. icarus* as their host. However, the most abundant parasitoid at the newly colonised sites (*C. astrarches*) is only known from one or possibly two other butterfly hosts in Britain (*A. artaxerxes* and less certainly *Cupido minimus* Fuessly; Shaw, 2007), neither of which are present in this part of Britain (although *A. artaxerxes*, *C. minimus*, and *C. astrarches* are all present further north). So this parasitoid might have expanded with *A. agestis*. At first sight it may seem surprising that a parasitoid species not previously present in the area would have become the most abundant parasitoid attacking the new host. However, Torchin *et al.* (2003) found that parasites that invaded with their host achieved as high prevalence in introduced populations as in their native populations, presumably reflecting the focus with which true specialists seek their host once they have arrived at a site. In the present study, the parasitoid has achieved an even higher level of attack in the newly established populations. It is possible that interactions between enemies might have affected the levels of parasitism by different parasitoids. Competition between *Hyposoter* and *Cotesia* species has been reported for the parasitoid assemblage associated with another butterfly species (*Melitaea cinxia* Linnaeus; van Nouhuys & Tay, 2001). These authors found that mortality of the parasitoid *Cotesia melitaearum*(-agg.) (Wilkinson) was higher in host caterpillars already occupied by the parasitoid *Hyposoter horticola* (Gravenhorst), probably as a result of larval competition. In our system both *Cotesia* species (*C. astrarches* and *C. saltatoria*) achieved lower parasitism on *A. agestis* caterpillars in long established populations where *H. notatus* achieved the highest parasitism rate on this host. In contrast, parasitism by *Cotesia* species was higher in newly colonised areas where *H. notatus* concentrated on another host, *P. icarus* caterpillars (see Table 1). In addition, there is the possibility that the newly arrived *Cotesia* is also experiencing *release* from its natural enemies; the enemy release hypothesis should apply to all trophic levels. There are many species of *Gelis* Thunberg (Schwarz & Shaw, 1999) and other cryptine ichneumonid genera (e.g. *Acrolyta* Foerster and *Lysibia* Foerster; Schwarz & Shaw, 2000) that parasitise *Cotesia* cocoons as generalists, although they may focus their search on productive microhabitats on a local basis. Thus, these hyperparasitoids might be failing to search for *Cotesia* cocoons on normally unproductive plants like *Geranium* and *Erodium* in the new colonised areas. Finally, knowledge of the parasitoid species attacking butterflies in Britain is still poor, so it is just conceivable that *C. astrarches* could actually have already been present

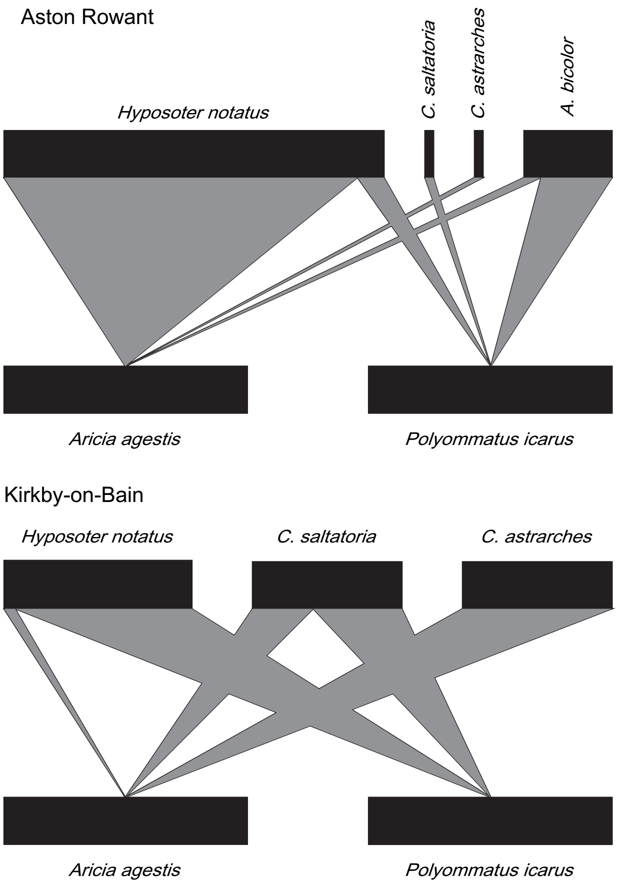

Fig. 5. Complex of parasitoid species attacking *Aricia agestis* and *Polyommatus icarus* caterpillars at Aston Rowant (both species long established) and Kirkby-on-Bain (colonised by *Aricia agestis* in 1995; *Polyommatus icarus* long established). The two series of bars represent the abundance of parasitoids (top) and butterflies (bottom). Butterfly abundance was assumed to be equal as no data were available. The widths of the links represent the relative frequency of each host–parasitoid association.

in the newly colonised areas but using alternative unknown (lycaenid) hosts.

2. Enemies are present in the newly colonised area but they are locally specialised on another host, such that they are literally not as able to use the new host, either as a result of a behavioural failure to accept it, or through physiological incompatibility (Kraaijeveld *et al.*, 1995; Geervliet *et al.*, 2000; Vos & Vet, 2004). In principle this could be a possibility in the case of *H. notatus*, the most common parasitoid of *A. agestis* in long-established populations. In newly colonised areas, this parasitoid mainly attacks *P. icarus* caterpillars, so it is possible that parasitoids from these populations are locally specialised on *P. icarus*. However, females of *H. notatus* from Kirkby-on-Bain, one of the newly colonised sites, did not exhibit any perceptible preference between *P. icarus* and *A. agestis* caterpillars when offered both host species in the absence of food plant under laboratory conditions (R. Menéndez & A. González-Megías, pers. obs.). As mentioned above, host recruitment is relatively common when exotic invaders move to an area that contains closely related native congeners (Keane & Crawley, 2002).
3. Finally, many parasitoids find their host by searching on the food plant used by the butterfly caterpillars (Vet & Dicke, 1992). If the colonising host is feeding on a host plant (*Helianthemum*, *Geranium*, and *Erodium* in the case of *A. agestis*) not used by other potential hosts present in the area (*P. icarus* caterpillars eat *Lotus corniculatus* and other Fabaceae), parasitoids may be not able to find the new caterpillar species because they are not searching in the right place. This is the most plausible explanation for all parasitoid species (except for *C. astrarches*) found in the present study, as *A. agestis* and *P. icarus* feed on completely different (although sometimes growing adjacently) host plants. It is well known that plant effects can be important in limiting the extent of parasitism both of a given host species on some of its food plants (Price *et al.*, 1980; Gratton & Welter, 1999; Heard *et al.*, 2006; and references therein) and of several host species that used different host-plants (Geervliet *et al.*, 2000). However, experimental work needs to be carried out to test this hypothesis for the present situation.

It seems that *A. agestis* is at least partially escaping from its enemies when colonising new areas. Although parasitoids are already present, using other hosts, these natural enemies are apparently relatively unsuccessful at locating the new host. Whatever the mechanism involved, the results show that *A. agestis* is experiencing reduced parasitism, declining from approximately half of the larvae sampled dying from parasitism in long-established populations to a quarter suffering this form of mortality in newly colonised regions. Because parasitoids are important regulators of host population dynamics (Hassell *et al.*, 1989; Hawkins & Cornell, 1994; Bonsall *et al.*, 2004), the colonising butterfly is likely to experience demographic release. It has been suggested that annual abundance cycles of other lycaenid butterflies in Britain, in particular *Celastrina argiolus* (Linnaeus) are likely to be driven by its specialist ichneumonid parasitoid *Listrodromuns nycthemerus* (Gravenhorst) (Revels, 1994, 2006). Additionally, Pollard *et al.* (1996) found that newly established populations of another expanding butterfly in Britain (*Pararge aegeria* Linnaeus) grew strongly in the early period of establishment, and they suggested that enemy release could be a potential explanation for this pattern.

Rates of range expansion will depend on dispersal ability, the sizes of populations that become established (affecting propagule number), and the intrinsic rate of population increase (*r*). Escape from parasitism may contribute to high levels of *r*, and hence result in increased rates of range expansion for the host.

In broad terms, the literature has tended in the past to emphasise the likelihood that interactions among species will reduce the abilities of species to exploit the full range of physical environments available, as the climate changes (Carpenter *et al.*, 1993; Ives, 1995; Davis *et al.*, 1998). The results of the present study suggest that the opposite may be equally relevant; that the decoupling of species interactions may allow some species to exploit a wider range of environments (Stireman *et al.*, 2005), and to do so more rapidly than previously thought possible.

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Appendix. Sampling localities in Britain.

Locality	Coordinates	Part of the range	Host plant
Aston Rowant NNR	SU727989	Old	*Helianthemum nummularium*
Incombe Hole	SP960155	Old	*Helianthemum nummularium*
Tring	SP929102	Old	*Helianthemum nummularium*
Malling Down SWT	TQ425105	Old	*Helianthemum nummularium*
Wytham	SP457081	Old	*Helianthemum nummularium*
Sandwich Bay	TR354600	Old	*Geranium molle/Erodium cicutarium*
Holme Dunes NNR	TF749442	Old	*Geranium molle/Erodium cicutarium*
Gwithian	SW574403	Old	*Geranium molle/Erodium cicutarium*
Barnack Hills & Holes NNR	TF075045	New	*Helianthemum nummularium*
Brockadale YWT	SE510172	New	*Helianthemum nummularium*
Ledsham YWT	SE460300	New	*Helianthemum nummularium*
Messingham LWT	SE912038	New	*Geranium molle/Erodium cicutarium*
Gibraltar Point NNR	TF565585	New	*Geranium molle/Erodium cicutarium*
Whisby LWT	SK910668	New	*Geranium molle/Erodium cicutarium*
Broughton	SE962104	New	*Geranium molle/Erodium cicutarium*
Kirby-on-Bain LWT	TF236609	New	*Geranium molle/Erodium cicutarium*

NNR, National Nature Reserve; SWT, Sussex Wildlife Trust; YWT, Yorkshire Wildlife Trust; LWT, Lincolnshire Wildlife Trust.