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Polymorphic growth rates in myrmecophilous insects

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A polymorphism in growth rates was recently described affecting the larval development of the myrmecophilous butterfly *Maculinea rebeli*, spanning different years in a single insect population. The close integration of *M. rebeli* into the host ant colonies, facilitated by adaptations in behaviour and chemical mimicry, make extended larval development a successful strategy. Here we present additional data for *M. rebeli* and new data for *Maculinea alcon* (another cuckoo-feeding lycaenid) and the two myrmecophilous predators *Maculinea arion* and *Microdon mutabilis* (Diptera: Syrphidae). As predicted, *M. alcon* shows the same growth pattern as *M. rebeli* with a proportion of caterpillars developing in one year and the remainder over two years. This pattern holds in both northern and southern European populations, where *M. alcon* exploits different species of host. Against expectation, the same bimodal distribution of pre-pupation body weights, indicating one and two year developers, was found for the larvae of *M. arion* and *M. mutabilis*. As predators, both species are less closely integrated in their host ant colonies, suggesting that the polymorphism in growth rates is a more general adaptation to a myrmecophilous life style, arrived at by convergent evolution between the *Maculinea* and *Microdon* species. For predatory species we suggest that biennialism is an adaptation to the migratory behaviour of the host made possible by the predators' ability to fast over extended periods. We also hypothesize that *M. arion* represents an ancestral strategy in *Maculinea* butterflies and that the growth polymorphism might have become genetically fixed in the cuckoo-feeding species.

Keywords: social parasites; growth polymorphism; myrmecophilous insects; ants

1. INTRODUCTION

An estimated 80 000–100 000 insect species have a myrmecophilous life style and live in close association with ant colonies. Most myrmecophiles are commensals or mutualists, while *ca.* 10% are obligate myrmecophiles, many of which live as social parasites (Elmes 1996). Ants are keystone organisms and local variation in how they function is likely to alter whole communities (Wilson 1990; Simberloff 1991). Thus, insight into the dynamics and evolution of ant–parasite associations also increases our understanding of whole community dynamics.

Thomas *et al.* (1998*b*) recently demonstrated that a single cohort of larvae drawn from a population of the myrmecophilous butterfly *Maculinea rebeli* (Hirschke) contains *ca.* 25% of individuals which develop and eclose within one year and 75% which develop over two years, irrespective of food supply, ambient temperature and other biotic or abiotic factors. These and further experiments (G. W. Elmes, unpublished data) strongly suggest that this represents a genetic polymorphism in larval growth rates. Although some other insects show genotypic variation in phenology between different populations across their ranges and individuals of certain boreal, montane or desert species can switch development from year to year as a phenotypic response to variation in temperature and seasonality (Schröder 1967; Carl 1972; Eichhorn 1982, 1983; Schönrogge 1991; Schönrogge *et al.* 1999), *M. rebeli* is the first insect thought to possess a fixed polymorphism of annual and biennial individuals within the same population. The only comparable example from the animal kingdom involves male salmonid fish (Gross 1985). However, their morphs, unlike those of *M. rebeli*, have strikingly different morphologies and behaviours.

The existence of biennialism in *M. rebeli* was unexpected because the species has none of the characteristics for which prolonged growth is predicted in insects, namely a large body, innutritious food, a short growing season and a stable although inhospitable environment (Taylor & Karban 1986; Stearns 1992; Charnov 1993; Williams & Simon 1995). In other species, the extended juvenile stage has been interpreted as a way of minimizing local extinction by catastrophic events ('bet hedging') (Hanski 1988; Hanski & Stahls 1990; Thomas *et al.* 1998*b*) or unusually short growing conditions. Thomas *et al.* (1998*b*) hypothesized that biennialism evolved in *M. rebeli* as an ergonomic adaptation which results in nearly double the number of eggs from an individual mother surviving to adulthood, although, once evolved, the mixture of annual and biennial morphs would have additional bet-hedging advantages.

We suggested that *M. rebeli* was pre-adapted for this trait to evolve due to a life style which ranks among the most specialized of any social parasite of ant colonies (Elmes *et al.* 1991*a*; Thomas & Elmes 1998; Thomas *et al.* 1998*a*). We considered the following features to be prerequisites.

(i) Larvae frequently reach such high levels of infestation within ant nests that their key mortalities occur through intraspecific, density-dependent, contest competition for food.
(ii) Their food supply is continually replenished, to a low ceiling, throughout the growing season.
(iii) Larvae achieve such close integration with their hosts that they are transported with the colony whenever the ants move nest site.
(iv) The spatial dynamics of host ant colonies and social parasites within a site are such that biennial larvae in their second year are infrequently exposed to competitive densities of the next generation of social parasite.

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M. rebeli populations have all four attributes (Thomas *et al.* 1998*a*,*b*). For example, after a brief period feeding on an initial food plant (the flowers of *Gentiana cruciata* L.), the small, newly moulted, fourth-instar larvae are adopted by foraging *Myrmica schencki* Emery workers and placed among the ant brood, where the nurse ants feed them by trophallaxis with trophic eggs and prey throughout autumn, spring and (in the case of biennials) summer. *M. rebeli* larvae infiltrate host colonies by secreting species-specific mimetic chemicals (Akino *et al.* 1999). They soon become so closely integrated with their host's society that they are carried and fed in preference to the ants' own larvae and are so well-protected that they experience few mortalities apart from (intense) intraspecific competition as they contest for worker attention and, hence, for food. For a variety of reasons, there may be no recruitment of new parasites into an occupied ant colony in the second year (for a review, see Thomas *et al.* 1998*a*). In *Myrmica* and other ants the presence of queens and brood are the determining factors for the persistence of a colony, without which workers disperse and often join neighbouring colonies (Elmes *et al.* 1998). The close mimicry of ant larvae by *M. rebeli* also promotes the persistence of the host colony until the parasites complete their larval development.

Thomas *et al.* (1998*b*) predicted that a few other myrmecophiles may have evolved this unusual annual–biennial polymorphism in response to ergonomic and social conditions in host ant nests. However, we thought this would be confined to other cuckoo-feeding social parasites such as *Maculinea alcon* (Dennis & Schiff.), a close relative of *M. rebeli*. We thought it unlikely to occur in *Maculinea arion* L. or, indeed in the majority of social parasites which are predators of ant brood or, in some case, of the trophobiont aphid herds. This was because their food exists for much of the year as a finite non-renewable resource within the ant colony, which in the presence of strong intraspecific competition can be easily exhausted before the completion of larval development by the predators (scramble competition) (Thomas *et al.* 1998*a*,*b*).

In this paper, we confirm that *M. alcon* has the same polymorphism as *M. rebeli*. However, we also provide evidence for a similar phenomenon in both *M. arion* and a myrmecophilous syrphid fly, *Microdon mutabilis* L. (order Diptera), which spends its entire larval life inside an ant nest where it preys upon ant larvae (Elmes *et al.* 1999). We therefore extend our hypothesis about which traits may lead to the evolution of polymorphic growth rates, making it more generally applicable to myrmecophilous social parasites.

2. MATERIAL AND METHODS

The material for this study was collected over a number of years and locations over a large geographical range. Fourth-instar *M. alcon* larvae were obtained by collecting stems of the larval food plant (*Gentiana pneumonanthe* L.) in early August. Judicious sampling has no negative impact upon the populations of these rare species (Thomas & Elmes 1993). They were transferred directly to small laboratory colonies created from wild nests excavated in the field. It has been shown that *M. alcon* uses three different *Myrmica* host ant species depending upon the population's geographical location (Elmes *et al.* 1994). Four populations were sampled from the northern half of its range (Denmark and The Netherlands), where the host is *Myrmica ruginodis* Nylander and two from the southern half (Spain) where the obligate host is *Myrmica scabrinodis* Nylander. Small cultures were maintained in the laboratory as described by Wardlaw *et al.* (1998). Caterpillars were kept individually with some ant brood and seven to 20 workers, except in the case of two samples from The Netherlands collected in 1994, when groups of eight *M. alcon* caterpillars were reared by 40 workers during autumn and were then kept individually by 20 workers in spring. After adoption each larva was weighed every week until pupation (usually during June of the next year). Cultures were maintained for a few weeks after pupation ceased, then most experiments were terminated because small cultures of *Myrmica* deteriorate after 12 months in the laboratory (Wardlaw *et al.* 1998). Any caterpillars which were alive and healthy two weeks after pupation ceased were assumed to be biennials as demonstrated for *M. rebeli* (Thomas *et al.* 1998*b*). This was also confirmed for *M. alcon* using a small number of cultures which were maintained for a second year.

We measured the body weights of 26 *M. arion* caterpillars, which were also collected from their initial food plants, using individuals which originated in France (Dordogne) and Sweden. With two exceptions, these were kept singly either in small boxes or using the 'walnut method' with their obligate host *Myrmica sabuleti* Meinert. All were provided with surplus food, but in four different diets/treatments: large ant larvae only ($n = 6$), ant pre-pupae only ($n = 6$) and under walnuts containing mixed ant brood and *M. arion* from France ($n = 5$) or Sweden ($n = 9$) (see Thomas & Wardlaw 1992). Since *M. arion* caterpillars are very sensitive to disturbance and because it is virtually impossible to rear them to pupation, all were weighed only once after eight weeks with ants, towards the end of the autumn growth period. In order to pool the data, we controlled for treatment effects by standardizing each data point by the means and standard deviation (s.d.) within each treatment.

Microdon mutabilis larvae were obtained by excavating host *Myrmica scabrinodis* nests from sites in Devon and Dorset (southern England) just prior to adult emergence during early May 1996–1999. A similar sample was taken of a population on the Burren, Ireland during May 1999. The Burren population was using *Formica lemani* Bondroit as its host ant, which belongs to a different subfamily and has a very different life cycle to *Myrmica* species. Therefore, we treated the two samples separately since they might represent different host races or even cryptic species (Elmes *et al.* 1999). We again categorized the larvae as 'fast' or 'slow' developers depending on whether they pupated the same spring or continued to develop for a second season (see § 4 for further interpretation of these categories). All the weights used for both *M. arion* and *Microdon mutabilis* were measured just before the 'fast developers' pupated.

To compare the new *Maculinea* and *Microdon* data to those of *M. rebeli* further, we used the body weight measurements of two *M. rebeli* caterpillars and 12 pupae collected from nests of *Myrmica schencki* Emery in 1999 in the Pyrenees in addition to the data published by Thomas *et al.* (1998*b*).

All tests and analyses were made using the MINITAB[1] statistical computational package, where the *t*-tests were performed assuming unequal within-group variances. For the weight distribution data of *M. arion*, where there is no independent evidence to divide the larvae into slow and fast developers, a test for mixed distributions was performed according to the mixture analysis by McDonald (1986).

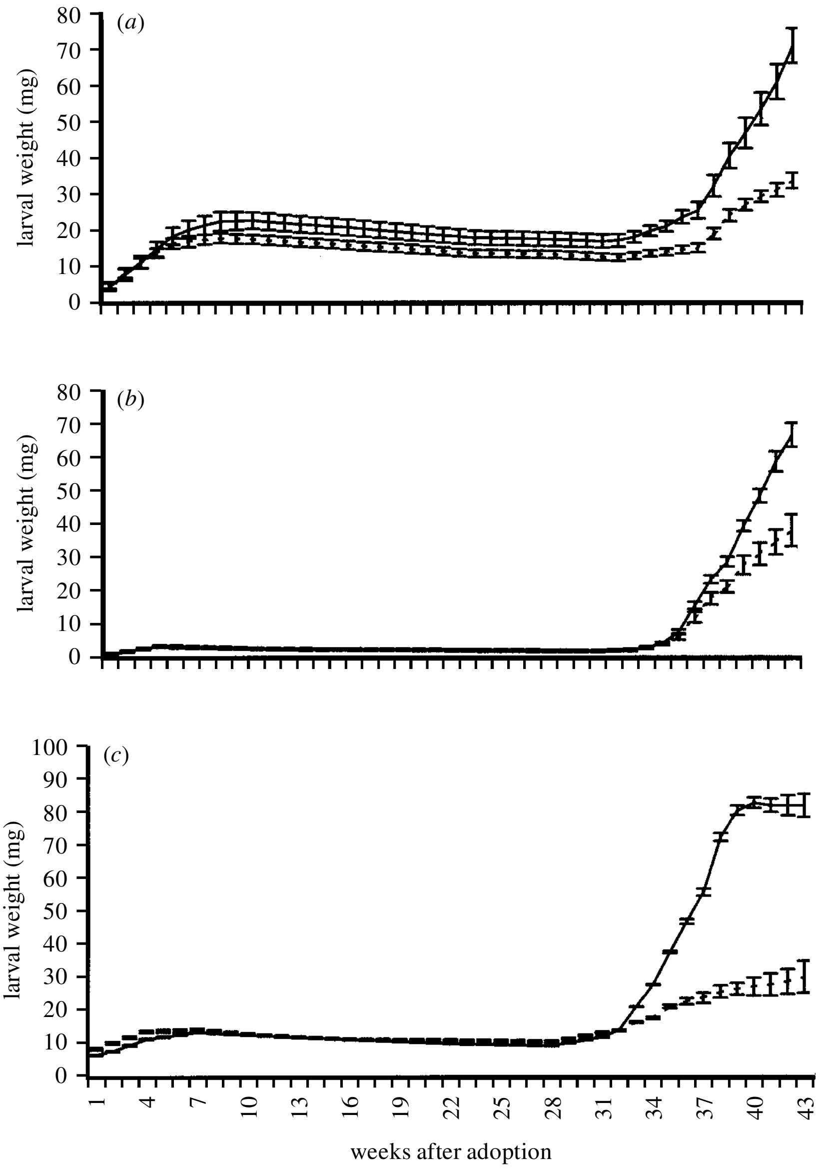

Figure 1. Body weight development between August and June of fast-developing (solid lines) and slow-developing (dashed lines) larvae of *M. alcon* (mean s.e.) from (*a*) Dutch and Danish sites, (*b*) from near Castro Urdiales (Spain) and (*c*) from near Soria (Spain). (*a*) Fast developers, $n = 22$ and slow developers, $n = 30$. (*b*) Fast developers, $n = 17$ and slow developers, $n = 7$. (*c*) Fast developers, $n = 5$ and slow developers, $n = 15$.

3. RESULTS

(a) *Development of body weights in* Maculinea alcon

The larvae from all locations developed into two distinct weight classes. The pattern of body weight development for the four northern sites, where *M. alcon* is associated with *Myrmica ruginodis*, was the same and the prepupation weights among fast and slow developers were similar (ANOVA fast developers, $F_{2,15} = 3.12$ and $p > 0.05$ and slow developers, $F_{2,26} = 1$ and $p > 0.05$). The data were pooled to calculate a common growth trace (figure 1*a*). The data from Spain, where *M. alcon* parasitizes colonies of *Myrmica scabrinodis*, showed greater geographical variation and the two traces are shown separately (figure 1*b*,*c*). The first measurements were taken one week after adoption when there was no significant difference between the weights of larvae which pupated between mid-June and mid-July the following year (fast developers) and those which stayed as fourth instars throughout the summer (slow developers). Three of the slow-developing larvae were successfully reared through their second winter and they pupated at a similar date to the fast developers only one year later.

In the northern European group, the fast developers gained 32% of their pre-pupation body weight (mean 71.0 mg) by week 10 (figure 1*a*). Thereafter the larvae entered winter dormancy during which there was a slight loss of weight until week 35, when a rapid increase in body weight began which continued until the pupation of the larvae (figure 1*a*).

In contrast, the slow developers gained only 24% of the fast developers pre-pupation weight in their first autumn (week 10) (fast- versus slow-developer weight $t = 2.0$, d.f. $= 33$ and $p = 0.05$). Like the fast developers they entered dormancy and showed a slight loss in weight until they increased in body weight again. However, they gained weight at a much more moderate rate compared to the fast developers and by the middle of June (just

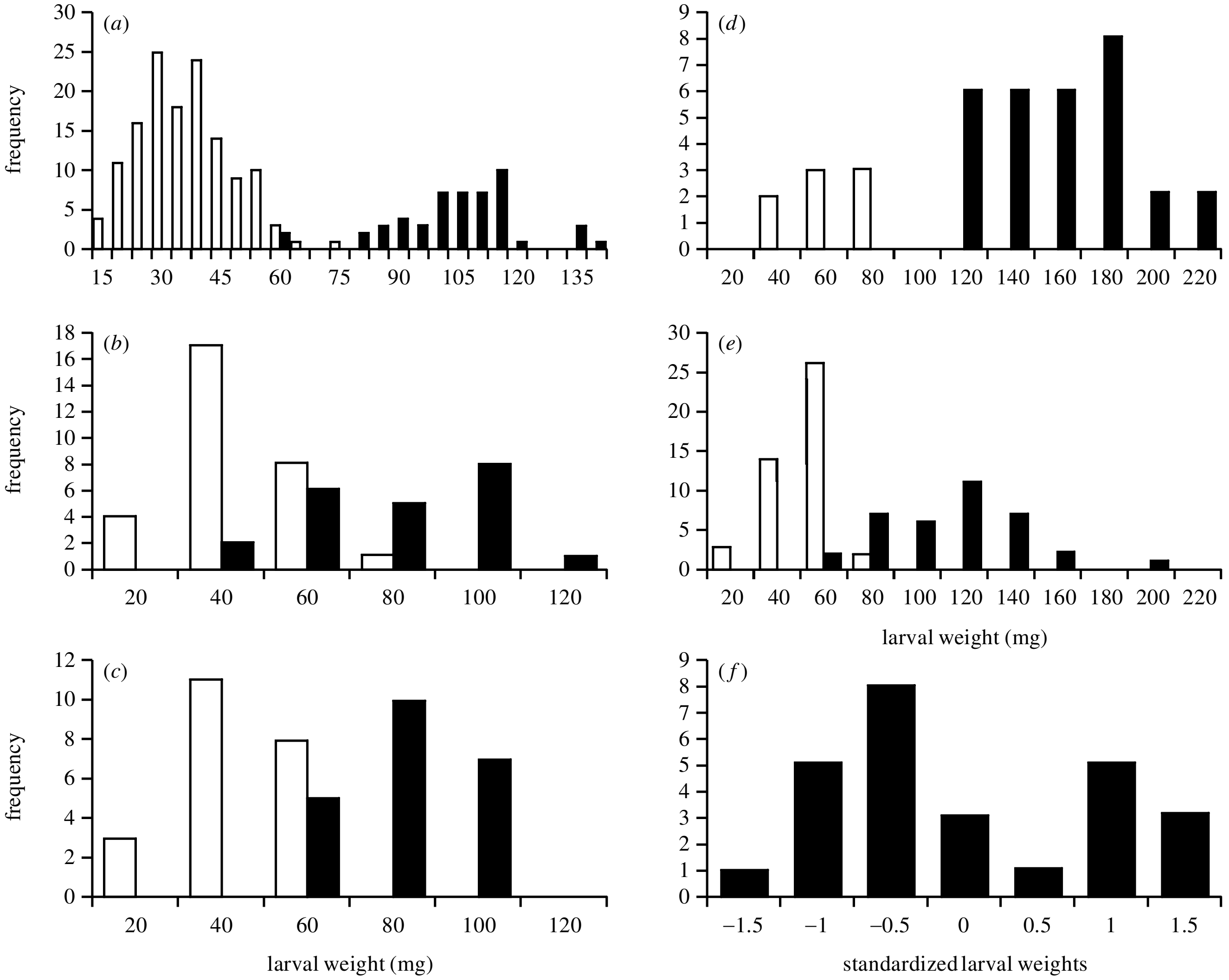

Figure 2. Frequency distributions of body weights at the fast developers pre-pupation time for (*a*) *M. rebeli* (based on Thomas *et al.* (1998*b*) with additional data), (*b*) *M. alcon* (northern European populations), (*c*) *M. alcon* (Spanish populations), (*d*) *Microdon mutabilis* (Irish population reared by *F. lemani*), (*e*) *Microdon mutabilis* (southern English population reared by *Myrmica scabrinodis*) and (*f*) standardized pre-hibernation weights of *M. arion*. Filled bars indicate fast developers and open bars slow developers.

pre-pupation of the fast developers) they had reached on average only 47.6% of the weight of the pupating larvae ($t = 7.06$, d.f. = 29 and $p < 0.001$) (figure 1*a*).

Unlike the larvae from the northern European group, those from Spain gained very little weight during their first autumn (< 5% of the pre-pupation weight of the fast developers) (figure 1*b*,*c*) and there was no significant difference between the slow and fast developers before the larvae entered winter dormancy. However, the following spring these larvae grew faster than those from the north European sites. By summer (week 44) there was no difference between the populations in the weights of either the fast developers (ANOVA, $F_{5,43} = 2.28$ and $p > 0.05$) or slow developers (ANOVA, $F_{5,45} = 1.69$ and $p > 0.05$) (but see § 3(b) for differences between the slow and fast developers).

(b) *Bimodal distributions of the pre-pupation body weights*

The body weight distribution for *M. rebeli* excavated from wild host nests at pre-pupation time showed a characteristic bimodal distribution due to the different rates of growth by slow- and fast-developing larvae (figure 2*a* and table 1).

The weight distributions for all six populations of *M. alcon* showed the same bimodality as *M. rebeli*. We pooled the data from the north European sites and from Spain and in both groups the fast developers were significantly heavier than the slow developers at the fast developers pre-pupation time (figure 2*b*,*c* and table 1).

The same bimodal distribution of body weights was found for both the Irish and English populations of the predatory syrphid *Microdon mutabilis* (figure 2*d*,*e* and table 1). The large larvae (fast in figure 2*d*) of *M. mutabilis* went on to pupate, whereas the small larvae (slow in figure 2*d*) did not pupate in the same season but matured normally through a second season. Small larvae found in spring have been reported to pupate at the same time but one year later (Donisthorpe 1927).

In contrast to the *Maculinea* species, the fast larvae of *Microdon mutabilis* from Ireland were significantly heavier than those from England ($t = 7.02$, d.f. = 67 and $p < 0.001$). There was no difference in the weights of the slow larvae ($t = 1.32$, d.f. = 9 and $p > 0.05$). Note that, while the populations are referred to by their geographical origin, the Irish population is associated with colonies of *F. lemani* while the English population predates in colonies of *Myrmica scabrinodis*.

Table 1. *Mean body weights taken just prior to the pupation of the fast developers for the fast and slow developers of* M. rebeli, M. alcon (*northern and southern populations*) *and* Microdon mutabilis (*Scottish and English populations*)

(All comparisons are between fast and slow developers within populations and all *t*-tests shown are significant at $p < 0.001$.)

species	population	fast/slow	*n*	mean ± s.e. (mg)	*t*	d.f.
M. rebeli	n/a	fast	50	101.50 ± 2.3	26.78	68
		slow	136	34.08 ± 1.0	—	—
M. alcon	north	fast	22	69.80 ± 4.6	7.33	29
		slow	29	33.10 ± 2.0	—	—
	south	fast	22	72.40 ± 3.5	9.55	39
		slow	22	30.70 ± 2.6	—	—
Microdon mutabilis	Irish	fast	35	150.90 ± 5.0	11.54	15
		slow	8	53.40 ± 6.8	—	—
	English	fast	36	102.90 ± 4.6	10.93	57
		slow	45	43.70 ± 2.8	—	—

The mean weight of *Microdon* biomass per ant *Myrmica scabrinodis* nest in May was 561.6 ± 66.0 mg ($n = 18$). Assuming the same feeding efficiency (Thomas & Wardlaw 1992) as of *M. arion* larvae which take one year to develop and that *Microdon* is an obligate predator of ant brood, this biomass is equivalent to a mean colony size for *Myrmica scabrinodis* of 1148 workers to support the predators. In fact, the average colony size for this species in the UK is 462 workers (Wardlaw & Elmes 1996). Although colony size was not established at the *Microdon* sites, we did not consider them above average. Nor was every nest supporting its full capacity of *Microdon*. Thus, the fact that 2.48 times the expected predator biomass was found per nest suggests that they represent the product of more than one nest and/or more than one year's feeding.

M. arion, like *Microdon mutabilis*, is predatory in ant colonies. Despite the early date when the body weights were measured, the distribution of standardized weights has only a marginal probability of originating from one normal distribution (mixture analysis, $\chi^2 = 10.55$, d.f. = 3 and $p < 0.05$), while it cannot be distinguished from two combined normal distributions ($\chi^2 = 0.19$, d.f. = 6 and $p > 0.5$). This is a clear difference even when considering the reduced reliability of the parameter estimates in the McDonald (1986) mixture analysis at small sample sizes. In addition, the frequency distribution shown in figure 2*f* suggests a bimodal distribution of body weights similar to those found for the cuckoo-feeding species of *Maculinea*.

4. DISCUSSION

These results indicate that *M. rebeli* is not unique among myrmecophiles in possessing polymorphic growth rates of annual and biennial larvae within the same population. As predicted, its close relative *M. alcon* shows this basic growth pattern both in the northern half of its European range, where it parasitizes *Myrmica ruginodis* and in the south where the populations are host specific to *Myrmica scabrinodis* (Elmes *et al.* 1994). Not only are the ecological, climatic and seasonal conditions very different in these two regions (as indeed they are between the two areas sampled in Spain), but evidence is accumulating that the *M. alcon* populations using these different species of host ant belong at least to different subspecies and perhaps to sibling species (Gadeberg & Boomsma 1996). Our original hypothesis about the evolution of a polymorphism in cuckoo-feeding myrmecophiles (Thomas *et al.* 1998*b*) therefore appears to be robust.

Extrapolation of the ergonomic hypothesis to predacious social parasites which undergo intense scramble competition for food has suggested that biennialism was unlikely to have evolved in such species (Thomas *et al.* 1998*b*). However, the results for the predacious larvae of *M. arion* and *Microdon mutabilis* contradict this prediction. Those for *Microdon mutabilis* establish that all populations studied contain at least some biennial larvae. This in itself was counter-intuitive, although we cannot exclude the possibility that *Microdon mutabilis* populations consist only of biennial larvae. If so, our categories slow and fast would refer to larvae in their first and second years. However, this seems unlikely with a small predacious insect which inhabits a temperate climate and has a rich food resource available for long periods of the year.

As with *M. alcon*, *Microdon mutabilis* could comprise two sibling species of hoverfly, one adapted to exploit *F. lemani* and the other *Myrmica scabrinodis* (Elmes *et al.* 1999). These host ants belong to different subfamilies which have very different patterns of brood production and growth: no larvae overwinter in *F. lemani* colonies whereas ant larvae grow much more slowly in *Myrmica scabrinodis* colonies and approximately half the annual production overwinters. Despite these apparently large differences in the presence and abundance of food (ant larvae) in host ant colonies, larvae of both forms of *Microdon mutabilis* have a biennial growth strategy.

In contrast, it is certain that some *M. arion* larvae eclose after one year. A few have been reared through in the laboratory (e.g. Frohawk 1924) and comparatively large numbers of adults have emerged in summer one year after young *M. arion* larvae were introduced to ant nests on new, unoccupied sites in the UK (Thomas 1999). The evidence for a biennial form is less certain and is largely circumstantial, because *M. arion* is much harder to rear in the laboratory than *M. rebeli* and *M. alcon* (Wardlaw *et al.* 1998). The small number we reared to hibernation showed a significant dichotomy in growth rate (figure 2*f*) although this is less clear-cut than at the comparable stage in *M. rebeli*. The average coefficient of variation of the weights of these half-grown *M. arion* larvae is 46% compared with 80% for *M. rebeli*; nevertheless, it is high compared with the 13% recorded for typical phytophagous lycaenid larvae (Elmes *et al.* 1991*b*). If the dichotomy in the pre-winter weights of *M. arion* (figure 2*f*) does represent fast and slow developers within the same cohort, then the majority of *M. arion* caterpillars, such as *M. rebeli*, have the potential for biennialism.

Three other anecdotal observations suggest that biennial individuals may exist in *M. arion*.

(i) An appreciable number of adult *M. arion* emerged in 1985 two years after the original trial reintroduction of *M. arion* larvae to the UK in 1983, despite intensive efforts to remove all of the easily caught adults in 1984 and despite the fact that none of its conspicuous eggs were found that year (Thomas 1994).

(ii) A small, second peak of adults typically emerges in populations approximately two weeks after the main emergence, possibly representing the two types of larvae.

(iii) Adult emergence dates become progressively earlier towards the northern climatic limit of *M. arion*'s European range (Thomas 1999). This is contrary to the expected trend, but could be explained if northern populations consisted largely of biennial (or slower) developing larvae and southern populations contained more annuals.

Within the family of Lycaenidae the *Maculinea* are the only species for which biennial larval development has been reported. According to the current *Maculinea* phylogenies (Fiedler 1991), predacious species such as *M. arion* represent the ancestral life history, whereas cuckoo feeding is seen as a derived trait. Despite Thomas *et al.*'s (1998*b*) suggestion that polymorphic growth rates have an adaptive value only for cuckoo-feeding species, our results suggest that they are part of an ancestral life history. Taken together, the results for *M. arion* and *Microdon mutabilis* suggest a similar polymorphism in growth to that described for *M. rebeli* and *M. alcon*. At the very least, a predacious social parasite from one order of insects (*Microdon mutabilis*) has the same unexpected biennialism found in two cuckoo feeders from another order (*M. rebeli* and *M. alcon*). This indicates a more general association of prolonged growth with myrmecophily and convergent evolution between myrmecophilous lycaenid butterflies and a syrphid fly.

We suggest that the selective force for polymorphic growth in predacious species remains ergonomic. It is known that *M. arion* is as isolated as *M. rebeli* from external enemies once inside an ant colony and that its larvae experience intense intraspecific competition for food, resulting in high density-dependent mortalities (Thomas & Wardlaw 1992; Thomas *et al.* 1998*b*). The lack of ant brood found in colonies of *F. lemani* and *Myrmica scabrinodis* nests containing dipteran pupae suggests the same is true of *M. mutabilis*. Thomas & Wardlaw (1992) showed that significantly more adult *M. arion* emerged from individual host nests than could be explained by the annual brood production of single colonies and for *Microdon mutabilis* we calculated that the mean biomass of larvae found per *Myrmica scabrinodis* nest in May was 2.5 times greater than the capacity of an average-sized colony of that ant in one year (Wardlaw & Elmes 1996).

We suggest that the system functions because migrations by ant colonies between neighbouring nest sites, combined with the ability of predatory social parasites to fast, allow the latter to use the broods of more than one host colony over one or more years. It is known that *Myrmica* colonies frequently disperse after *M. arion* has destroyed their brood because their normal social focus has been lost and the *M. arion* caterpillar (unlike those of cuckoo-feeding *Maculinea* species) is not treated as a substitute (Thomas & Wardlaw 1992). Under these circumstances, the caterpillar is left behind in the empty nest where it awaits the arrival of an offshoot of a neighbouring host ant colony. *M. arion* larvae have an exceptional ability to fast once a certain biomass has been attained, enabling them to survive the waiting periods in vacated nest sites until fresh supplies of food are carried in: Thomas & Wardlaw (1992) estimated that up to 80% of *M. arion* adults result from caterpillars which have fed in this way. This behaviour has not been quantified in *Microdon mutabilis* but, like *M. arion*, we have never seen its later instars carried by ants and individuals are able to survive for weeks without food in the laboratory. In general, nest switches by ants are believed to be most common in spring, particularly among polydomous, polygynous species of ant such as *F. lemani* and all *Myrmica* species (Elmes *et al.* 1999).

Although the combination of starving ability by the predator and spatial dynamics of ant colonies was originally considered to explain the unexpectedly high capacity of single host nests observed for this predator, we now suggest that the same phenomenon may lead to biennialism or to polymorphic (annual–biennial) growth rates in any predacious species of social parasite which (i) is not very closely integrated with its host ant colony, (ii) has the ability to sustain prolonged periods of starvation, and (iii) parasitizes species of ant which live at high densities in polygynous, polydomous colonies which regularly switch nest site.

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