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Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies

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Caterpillars of *Maculinea rebeli* have two growth strategies for living underground as social parasites of *Myrmica* ant colonies. Laboratory experiments and field data show that 25% of caterpillars live ten months with ants before pupating, whereas 75% grow slowly, parasitizing their hosts for 22 months. Both types of caterpillar form apparently identical similar-sized pupae. This may be the first description in the animal kingdom of polymorphic growth rates spanning different years within the same population, yet without resulting (as in salmonid fish) in two morphologically distinct adult types with obvious differences in behaviour. We suggest that a balanced polymorphism has evolved in *M. rebeli* growth rates, representing the most efficient way of exploiting the limited, yet steady, daily supply of food available to cuckoo-feeding parasites of long-lived ant societies. Bet-hedging benefits would also accrue to adult butterflies producing a mixture of annual and biennial offspring. Despite ergonomic and other benefits, partial biennialism is unlikely to evolve unless slow-growing individuals have enhanced survival and can remain attached to their mobile hosts. We show that caterpillars become so closely protected by, and integrated with, their host colonies that slow growers experience no greater mortality over two years than fast growers over one, and are transported in preference to the ants' own larvae when the host colony moves nest site.

Keywords: larval growth; competition; development; myrmecophily; social parasitism

1. INTRODUCTION

Few insects are known or expected to have juvenile periods lasting for more than one year (Stearns 1992; Charnov 1993). Species that do, generally possess one or more of these attributes: large bodies, innutritious food, short growing seasons and inhabit stable—if inhospitable—environments (Taylor & Karban 1986; Stearns 1992; Williams & Simon 1995). Certain slow-growing insects have juvenile periods that can vary phenotypically by one or more years; a few show inherent variation across their ranges (Wigglesworth 1964; Denno & Dingle 1981; Williams & Simon 1995). However, it appears exceedingly rare for any organism to exhibit a balanced polymorphism in growth rates within a population; salmonid fish (Gross 1985) may be the only example described among animals.

Although the butterfly *Maculinea rebeli* Hir. does not possess any trait hitherto associated with prolonged growth, Elmes *et al.* (1991*a*) speculated that annual and biennial individuals might coexist within its populations. This would be a unique lifestyle among Lycaenidae. However, the Palaearctic genus *Maculinea* is already known to possess extraordinary adaptations that enable its caterpillars to parasitize ant colonies (see Thomas *et al.* (1998) for a review). Females of all six species oviposit on the inflorescences of specific plants, which flower only in midsummer. The young caterpillars develop quickly to the fourth and final instar before leaving their food-plants in August. They then mimic the larvae of *Myrmica* ants and, after being found and adopted by foraging workers, live for 11 months inside *Myrmica* nests, where they obtain more than 98% of their final biomass by feeding in one of two ways. Caterpillars of *M. rebeli* and *Maculinea alcon* Denis & Schiff. continue to mimic ant larvae and are fed directly by nurse ants on regurgitations and prey (cuckoo feeding), whereas the others, including *Maculinea arion* L., eat only the ant brood.

The predacious caterpillars of *M. arion* are almost certainly univoltine. They frequently experience high mortalities through intraspecific competition for ant brood, which is a finite resource that is not replaced once it has been consumed (Thomas & Wardlaw 1992). But caterpillars of cuckoo *Maculinea* are treated like ant larvae, whose food supply is demand-led and available daily from March to November (Brian 1955). Only when demand exceeds the foraging capacity of the workers do caterpillars and the ant brood compete; ant larvae are the first losers, then at higher densities the caterpillars contest intraspecifically for food (Elmes *et al.* 1991*b*).

We hypothesized that partial biennialism might evolve in *M. rebeli* as an ergonomic adaptation to its population structure and style of feeding, for the following reasons. When a colony of the host ant, *Myrmica schencki* Emery, is situated within 2–3 m of a flowering *Gentiana cruciata* L. (the initial food-plant), it usually adopts many more

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caterpillars than can be reared in a single year (Thomas *et al.* 1998). Individual caterpillars that would lose the contest for worker attention could benefit if they fed little and grew slowly while demand from more competitive individuals was high. However, this would produce adults too late to oviposit on *G. cruciata* flower-buds, unless these individuals parasitized their long-lived ant colonies for a second year. Such caterpillars would experience reduced competition in the second year unless their hosts adopted a fresh cohort of caterpillars, which may not occur often on typical sites with low densities of gentians for the following reasons.

1. There is a minimum 10% annual turnover in the plant population, and variation in flower production and phenology makes some surviving gentians unsuitable for oviposition in consecutive years.
2. *Myrmica* colonies often move to new nest sites between years, especially when weakened by *M. rebeli* (Thomas *et al.* 1998), taking many away from flowering gentians.
3. Static but weakened *Myrmica* colonies generally have smaller territories that may not encompass the gentians in a second year.

The final prerequisite for this trait to evolve is that biennial caterpillars are well protected and remain firmly attached whenever their host colony moves.

The only previous evidence for our hypothesis was that the growth of *M. rebeli* caterpillars early in their final instar varied more than in any known lycaenid (Elmes *et al.* 1991*a*), and from unpublished observations of apparently bimodal growth among 26 caterpillars reared in two large observation nests of *Myrmica schencki* containing very different ratios of caterpillars to ants (figure 1*a*,*b*). Here we present field and laboratory evidence establishing polymorphic growth in *M. rebeli,* and show that caterpillars are so closely protected by, and integrated with, their hosts colonies that they have high survival over two years and are transported like ant brood when colonies move.

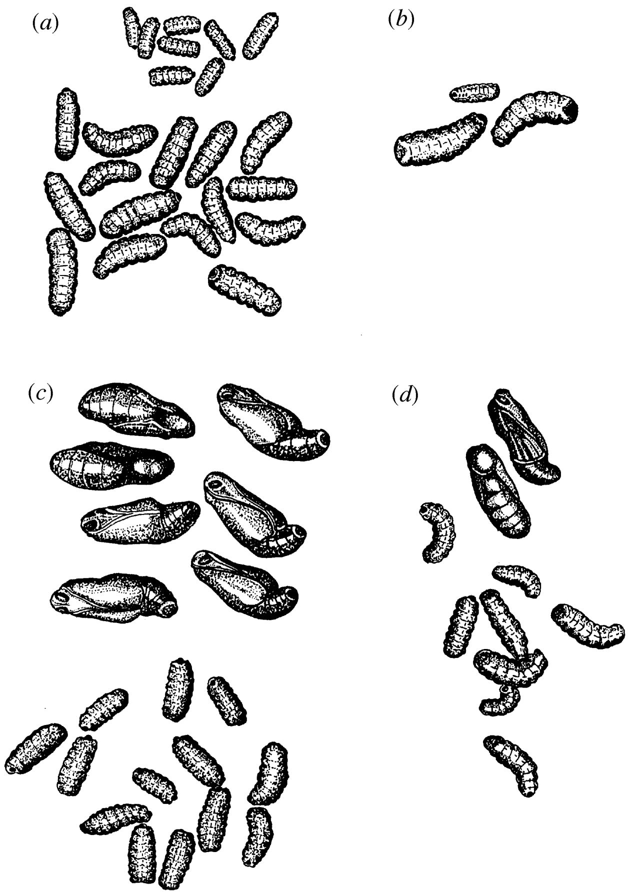

Figure 1. Scale drawings from photographs of *Maculinea rebeli* caterpillars from single *Myrmica schencki* nests. (*a*, *b*) Contents of captive nests 80 days after average and low densities of caterpillars were introduced: (*a*) 23 caterpillars with a colony of 913 ants (1:40 ratio); (*b*) 3 caterpillars with 951 workers (1:317 ratio). In both nests, only the large individuals pupated (*ca.* 250 days after introduction), but seven of the nine small caterpillars survived a further 106 days, when the trial ended. (*c*, *d*) Contents of typical wild nests excavated in July in the Pyrenees (*c*) and Alps (*d*). Note that pupae are 10% smaller than prepupal larvae.

2. METHODS

(a) *Field data*

Nests of *Myrmica schencki* were excavated on three *M. rebeli* sites in the French Alps (six nests) and on one in the Spanish Pyrenees (15 nests) at the onset or within the two weeks preceding adult emergence in 1990–1996. Every *M. rebeli* pupa and caterpillar found in them was weighed using a Sartorius field balance, accurate to 10^{-5} g, and 64 caterpillars from France and 32 from Spain were removed and reared in laboratory ant cultures to follow their development.

(b) *Growth rates in laboratory nests*

Growth rates of 1082 final-instar *M. rebeli* caterpillars were measured for up to 10–22 month periods in standard laboratory nests containing *Myrmica* (Wardlaw 1991), using livestock collected in the Alps or Pyrenees. Small replicated cultures of host worker ants were established, to which caterpillars were introduced within 12 h of their final moult. Cultures had abundant food and approximately natural daily and seasonal cycles of light and temperature, including a winter hibernation period (Wardlaw 1991). Caterpillars were individually weighed, each week when temperatures exceeded 14 °C and every 20–30 days in winter.

The main experiment involved rearing groups of between one and five *M. rebeli* caterpillars from France, in nests containing 40–100 *M. schencki* workers. At these densities, caterpillars pupated at similar dates and weights to those in the wild, and the results were not obscured by density effects (Elmes *et al.* 1991*a*; Thomas *et al.* 1993). The remaining 754 individuals were also weighed during experiments designed to explore other aspects of *M. rebeli*'s biology (Elmes *et al.* 1991*a*,*b*). These results were also analysed, using Macdonald's (1980) optimization routine, to determine whether their weights had polymodal frequency distributions and, if so, the minimum number of distributions that described the log-transformed data.

(c) *Competition between one-year-old and newly recruited caterpillars*

Experimental nests were set up to examine whether one type of caterpillar 'won' or 'lost' when young (1–2 mg) fourth-instar caterpillars were adopted into host colonies containing half-grown (21–58 mg) biennial caterpillars which had been adopted in the previous year. Forty-seven cultures were established in laboratory nests from *M. schencki* colonies containing biennial caterpillars excavated from the Alps in 1996. Each was kept under the semi-natural conditions described above, and contained 40 workers, ten large ants from the brood and its own half-grown *M. rebeli* caterpillar(s). Thirty-one nests were set with one half-grown caterpillar to which one freshly moulted caterpillar was introduced; 16 nests had two caterpillars of each type. The young caterpillars were collected from gentians on the same site as the old ones. Caterpillar survival and growth was recorded until 14 days after the last old biennial caterpillar had pupated.

(d) *The aptitude of* Myrmica *workers to transport* Maculinea *caterpillars to new nests*

Experimental ant nests were established within 4400-cm^3 plastic boxes for both *M. rebeli* (cuckoo feeder) and *Maculinea arion* (predator), with one nest per box. Each nest was an upturned 100-cm^3 flowerpot saucer with an entrance notch, placed over a small moist sponge pad. Our hypothesis was that the caterpillars of cuckoo *Maculinea* (i.e. *M. rebeli*) would be carried like ant brood if their nest was disturbed, but that those of predatory *Maculinea* (i.e. *M. arion*) would be abandoned. Both butterflies were tested only with their natural hosts, *Myrmica sabuleti* (four nests) in the case of *M. arion*, and *Myrmica schencki* (two nests) with *M. rebeli*. Each *M. sabuleti* 'colony' contained ten worker ants, ten large ant larvae, and ten small ant larvae (no pupae or prepupae were available); those with *M. schencki* contained ten workers, five pupae, five large ant larvae and five small ant larvae. When introduced, the workers quickly assembled their brood under the saucer. Freshly moulted final-instar *Maculinea* caterpillars were introduced 24 h later, one per nest in the case of *M. arion* and five per nest with *M. rebeli*, simulating typical densities for each species in the field. After another 48 h, each nest site was moved by lifting the saucer off the ant colony and placing it over another moist pad 20 cm away. The number of *Maculinea* caterpillars and ants from the brood of each type that were carried by the workers into the new nest site within 15 min was recorded, as was the order in which each was taken in. Twenty disturbances were made for each species, with a minimum of 4 h between each disturbance. The median order in which pairs of items were transported after each disturbance was compared using a non-parametric Wilcoxon Signed-Rank test.

3. RESULTS

(a) *Field evidence of biennial development in caterpillars*

The *M. schencki* nests excavated at the onset of adult butterfly emergence contained a mean of 8.4 (s.e. 2.8) *M. rebeli* per nest. Most (67%) nests contained two distinct size classes of *Maculinea*: pupae and comparatively small larvae (figures 1*c*,*d* and 2), at an average ratio of 1 pupa to 3.4 small larvae. Their weight distributions indicate a negligible chance that both stages were drawn from one rather than two cohorts of individuals (Macdonald's optimization routine, $p < 0.0001$). Because no hatched eggs of *M. rebeli* could be found on gentians at this time, and as eight weeks growth is required to attain the size of the smallest caterpillar found, we can conclude that all the *M. rebeli* had entered their ant nests no later than August of the previous year(s). The mean weight of caterpillars was 34.4 mg and that of the pupae was 100.5 mg, a ratio of 1:2.9 in individual weights between the two stages. This makes the average biomass of caterpillars and pupae similar (1:0.95) in *Myrmica* nests in July, when adjusted for an approximate 10% weight loss that occurs during pupation (Thomas & Wardlaw 1992).

Only one of the 96 caterpillars found in *M. schencki* nests at or after *M. rebeli*'s pupation dates pupated in the same summer, when rearing was continued in captivity. It contained a parasitoid, *Ichneumon eumerus*, which typically emerges two to three weeks after *M. rebeli* (Thomas & Elmes 1993). The other (unparasitized) caterpillars grew slowly during autumn and spring, and pupated and eclosed on dates typical to the field the following year, a minimum of two years after their original adoption by *Myrmica*. The 24 individuals that were aged above one year and that survived to pupate attained similar weights (63–121 mg) to the pupae found in their original wild nests in the previous year.

These observations suggest that some *M. rebeli* caterpillars follow a two-year development cycle in the wild. They do not preclude the possibility that all *M. rebeli* caterpillars take two years to develop, but the strongly unimodal weight distribution of the caterpillars in any one year (figure 2) makes it unlikely that additional cohorts exist living for more than two years.

(b) *Laboratory evidence for two growth rates*

In *Myrmica schencki* colonies given abundant food, every freshly moulted *M. rebeli* caterpillar developed in one of the two ways, as in figure 1*a*,*b*, with many nests containing both types of caterpillar: individuals either grew quickly during autumn and spring and pupated the following May/June, or they grew slowly and did not pupate in their first summer. The slow developers continued to grow for a minimum of eight weeks after the fast-growing individuals had pupated, at which stage most experiments were stopped owing to the near impossibility, with current knowledge, of keeping laboratory cultures of *Myrmica* healthy for more than 18 months (Wardlaw 1991). We retrospectively treated the 39 *M. rebeli* larvae that pupated in their first summer as one class, and the 67 (healthy looking) individuals that did not pupate, and which survived at least another eight weeks, as another. The weight changes of both classes over the preceding 12 months are plotted in figure 3 (black symbols). Following on from the slow-growing individuals, we depict the cohort of half-grown caterpillars that were excavated in wild *M. schencki* nests in France during August 1996 (figure 2) and reared on under identical laboratory conditions using their own ants in fresh cultures (figure 3, open symbols). These caterpillars had similar weights on the same dates in midsummer to the slow-developing laboratory caterpillars, and complete the growth pattern of this cohort. It is worth noting that one laboratory nest from Spain remained reasonably healthy for two years and reared a pupa that produced an apparently healthy adult after 22 months in the nest. This is our only direct observation of a two-year growth period in *M. rebeli*.

On average, fast-developing caterpillars increased from 2 mg to 62 ± 14 mg in autumn (weight$_A$), lost 20 mg (about 32%) of their weight over winter, but acquired a further 40 mg during spring to pupate after about 40

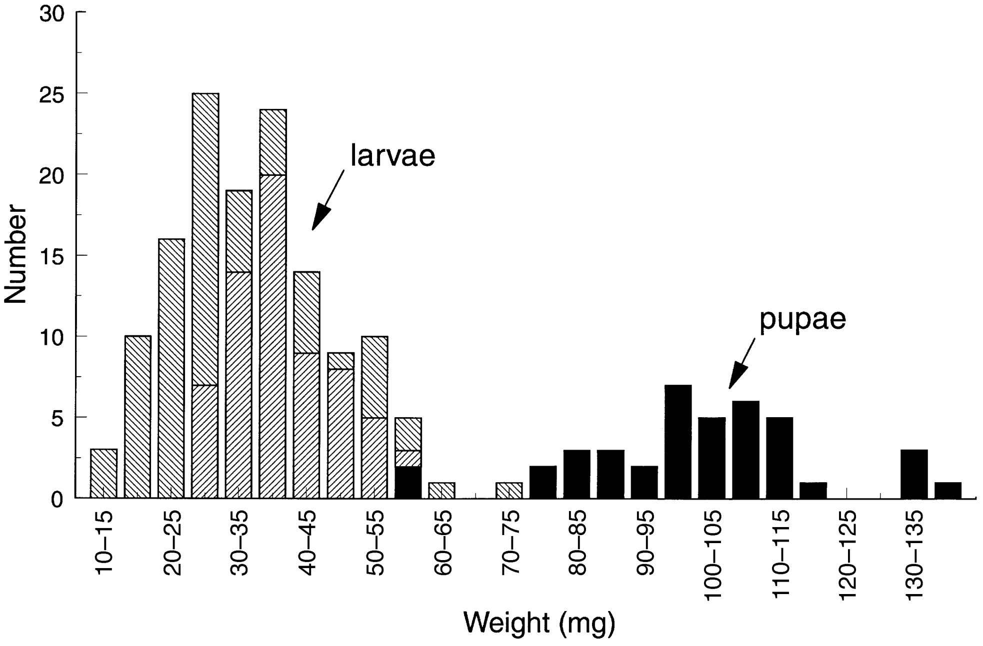

Figure 2. The weights of all *M. rebeli* caterpillars ($n = 136$) and pupae ($n = 40$) in wild *Myrmica schencki* nests at the onset of adult emergence in the Pyrenees (left-slanted hatching) and Alps (right-slanted hatching).

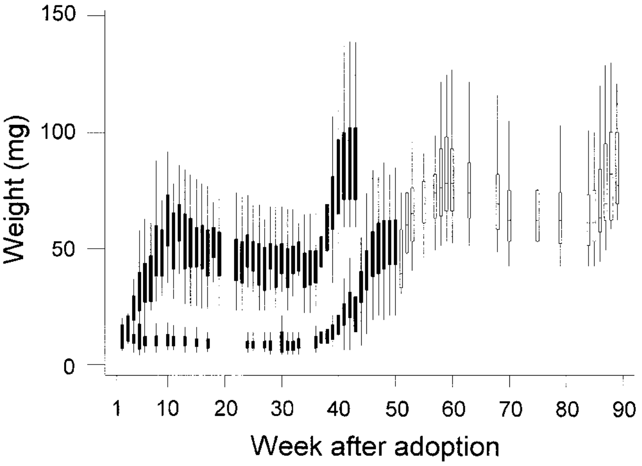

Figure 3. Growth rates of *Maculinea rebeli* caterpillars in laboratory nests containing surplus *Myrmica schencki*. Bars and fine lines represent the 50% and 95% distribution of weights in each cohort. Black bars indicate growth in the first 51 weeks after entering the final instar ($n = 106$): individuals pupating in May/June were assigned to one cohort, and those remaining as healthy caterpillars in August to the other (see text). Open rectangles show the growth of 66 11-month-old caterpillars (figure 2) that were collected from wild nests at adult butterfly emergence, and set in fresh laboratory nests.

weeks in the nest at a weight of 82 ± 16 mg. Slow-developers, on average, acquired exactly 25% of their ultimate weight after 40 weeks, and grew slowly through summer and autumn, reaching 82 ± 20 mg at the onset of the second winter. They grew rapidly during the second spring, restoring the 23% weight lost during hibernation, and finally pupated at an average weight of 88 ± 20 mg, which is not significantly greater than the average weight of fast-growing laboratory pupae ($t_{14} = 0.91$, $p = 0.38$).

Despite the wide range of laboratory conditions under which many other caterpillars have been reared (Elmes *et al.* 1991*a*,*b*), a distribution analysis of the weights of *M. rebeli* at the onset of their first winter consistently showed the same pattern of growth (table 1). This is clearest when subsets of the data are considered. A bimodal distribution best describes caterpillar weight$_A$—and a unimodal distribution is a very poor description—regardless of whether *M. rebeli* was reared with *M. schencki* or non-host species of *Myrmica*, or whether experiments are combined by years (table 1). Taking all these varied conditions together, there is a negligible chance (Macdonald's optimization routine, $p < 0.0001$) that the observed distribution was from a single normal population, whereas there was no reason to reject the hypothesis that it comprised a mixture from two normal distributions (table 1). Overall, the data are best described by a mixture of 74% slow-growing individuals (mean weight$_A$ = 10.4 mg) and 26% faster-growing ones (mean weight$_A$ = 42.2 mg), which is similar to the ratio of 3.4:1 small larvae (mean weight = 34.4 mg) to pupae (mean weight = 100.5 mg) found shortly before adult butterfly emergence in wild *M. schencki* nests (figure 2).

(c) *Competition between one-year-old and newly recruited caterpillars in ant nests*

No obvious winner or loser emerged when *Myrmica schencki* colonies containing half-grown two-year developing caterpillars recruited in 1995 adopted new caterpillars in August 1996. Twenty-two (35%) caterpillars from the older (1995) cohort and 25 (40%) individuals from the new (1996) cohort survived to the pupation period in May 1997. The new caterpillars experienced the usual high mortalities while integrating with *Myrmica* shortly after adoption, (Elmes *et al.* 1991*b*), but thereafter had lower mortalities than in the old cohort. Of course, this new cohort itself consisted of a mixture of one- and two-year developers, and although we could not discriminate between them for 17 days, we assumed they occurred in the overall ratio of table 1. Although the number of one-year developers was small, the results show that the 81% mortality in this class was significantly greater than that of new two-year developers (53% mortality;

Table 1. *Statistics of fit for modality in the weight distributions of* Maculinea rebeli *caterpillars after ten weeks in laboratory* Myrmica *nests, grouped by host ant species and year*

(n is the number of caterpillars. p_{uni} and p_{bi} are the respective probabilities that the observed distributions were drawn from one or two log-normal distributions. R is the estimated proportion of individuals in the smaller-sized category, assuming a mixture of two distributions. μ_1 and μ_2 are estimated mean weights (mg) of the slow- and fast-growing caterpillars, respectively. Differences in R between years are not statistically significantly (multiple-cross t-test).)

	n	p_{uni}	p_{bi}	R (s.e.)	μ_1 (s.e.)	μ_2 (s.e.)
all caterpillars	754	<0.00001	0.063	0.74 (0.02)	10.4 (0.3)	42.2 (2.0)
nurse species of ant						
Myrmica schencki	472	<0.00001	0.324	0.74 (0.03)	10.3 (0.4)	40.8 (2.3)
other *Myrmica*	282	<0.0001	0.012	0.75 (0.03)	10.8 (0.4)	45.7 (3.1)
year of experiment						
1984	74	0.0002	0.166	0.53 (0.11)	11.8 (1.0)	45.6 (6.5)
1987	272	<0.0001	0.171	0.73 (0.03)	10.7 (0.4)	49.6 (2.6)
1988	125	0.213	0.728	0.67 (0.29)	10.2 (1.4)	30.6 (7.6)
1991	58	0.0007	0.146	0.65 (0.22)	10.8 (37.0)	41.2 (7.6)
1993	211	<0.00001	0.058	0.86 (0.09)	10.0 (0.6)	29.9 (9.3)

$\chi_1^2 = 3.93$, $p < 0.05$), with the old (1995 intake) of two-year developers experiencing an intermediate mortality of 65%. These mortalities correlate with the increase in biomass—and hence the resources exploited—by these three classes of caterpillar during this experiment. The highest mortalities among one-year developers occurred during the phase of rapid growth before pupation. Whereas, few young two-year developers died after the initial period of integration into ant colonies. Combining the figures for the two cohorts of slow developers indicates that they experience a similar mortality (84%) over their whole two-year exploitation of *Myrmica* nests to the 81% mortality estimated for one-year developers in these same experiments.

(d) *The aptitude of* Myrmica *workers to transport* Maculinea *caterpillars to new nests*

When their experimental nest sites were moved, the workers of both *Myrmica schencki* and *M. sabuleti* carried all their own brood into the new nests within 15 min of every disturbance, a total of 239 transportations for the combined experiments involving *M. schencki* and 399 for *M. sabuleti* (the lack of round figures is explained by the death of a few *Myrmica* larvae during experiment). All *Maculinea rebeli* larvae were also carried into the new nests by nurse ants, a total of 100 transportations of the ten caterpillars. In contrast, none of the *M. arion* caterpillars was moved out of 80 possible transportations, even though, having carried their own brood into the new nest site, up to seven *Myrmica sabuleti* workers returned to search the old (exposed) nest. They frequently encountered the *M. arion* caterpillars but always ignored them. On four occasions, during the initial confusion after the removal of their nest lid, an ant tried to pick up a *M. arion* caterpillar, but each time the caterpillar gripped the substrate, and although the ant at first pulled hard, it soon abandoned the caterpillar.

Despite a considerable overlap in the order of transportation (figure 4), *M. schencki* workers picked up and transported the *M. rebeli* caterpillars and their own pupae first with an equal probability ($p = 0.46$), whereas large and small ant larvae were recovered significantly later ($p = 0.001$ and $p < 0.001$, respectively).

4. DISCUSSION

These results establish that *Maculinea rebeli* populations contain a mixture of caterpillars that take either one or two years to develop in the same host-ant colonies. Two-year developers form similar sized (possibly heavier) pupae and appear to have similar (possibly lower) survival over two years compared with fast developers over one year. Assuming equal survival, our results (figures 2 and 3 and table 1) suggest that about 75% of a *M. rebeli* adult population consists of individuals that took two years to develop and 25% that took one year.

Phenotypic variation reinforced by selective feeding by worker ants could result in two size classes of caterpillar, but these results suggest that it is probably a consequence of a genetically controlled polymorphism. Caterpillars are strongly unimodal in weight when adopted by ants (Elmes *et al.* 1991*a*), yet they can be clearly identified as fast or slow developers after three weeks with *Myrmica*, long before food shortages limit growth or cause differential mortality (figure 3). Moreover, similar ratios of slow to fast developers were obtained with different species of *Myrmica* and in different years (table 1), despite the wide range of caterpillar/ant densities and other conditions under which *M. rebeli* was reared (Elmes *et al.* 1991*a*). Further experiments are in progress to test the hypothesis that the polymorphism is genetically rather than phenotypically controlled. At present, we know of only one other species, the fish *Oncorhyncus kisutch,* in which a balanced polymorphism in growth rates spanning more than one year exists within a population. Major differences in lifestyle and morphology exist between the two growth forms of this salmon (Gross 1985); in contrast, we have observed none between the two forms of *M. rebeli,* although physiological and microscopic morphological differences may exist. A closer parallel is the growth of larvae of *Myrmica* ants themselves, which show an analogous bimodality albeit over a shorter time span: some

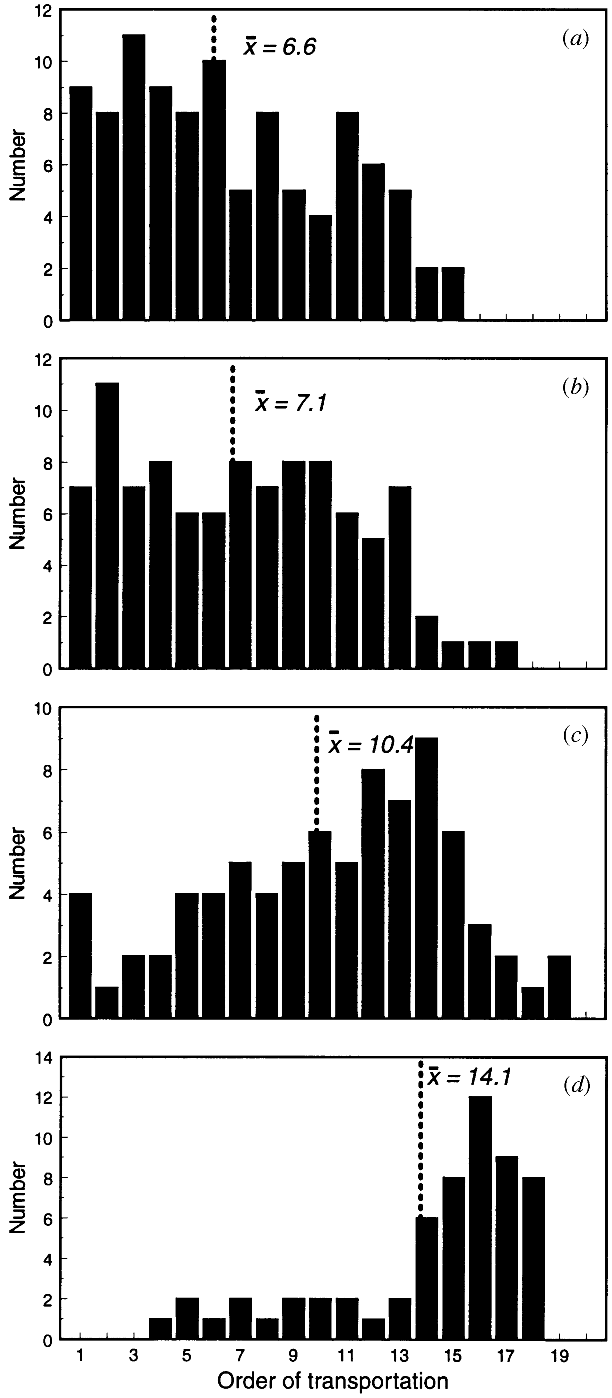

Figure 4. The order in which workers of *Myrmica schencki* recovered their pupae (*b*), large larvae (*c*) and small larvae (*d*), and *Maculinea rebeli* caterpillars (*a*) after their nest-box was moved. In each run there were up to 19 *Myrmica* brood or *Maculinea* to be transported by ten worker ants; the *x* axis indicates the order in which each type was transported.

larvae develop slowly and must experience winter diapause before metamorphosis, whereas others grow rapidly and pupate after a few weeks of development (Brian 1955). This bimorphism in *Myrmica* growth is a consequence of the complex interactions between larvae and workers involved in caste determination (Brian 1955). There is no reason to suppose that these affect the growth of *M. rebeli* caterpillars.

Although *M. rebeli* does not possess any described trait associated with prolonged larval growth, we suggest that ergonomic and bet-hedging benefits would accrue from its evolution in a system involving the exploitation of long-lived ant colonies by cuckoo-feeding social parasites. Thus *Maculinea alcon* may also show polymorphic larval growth. We favour the ergonomic argument, described in § 1, because our results suggest that exactly half the biomass of *Maculinea* supported by a wild *M. schencki* colony pupates in the first year and half remains for the next, more than doubling the potential number of butterflies from a season's intake that an individual ant colony can support. This trait is most likely to evolve if individual ant nests have a low probability of adopting caterpillars in consecutive years, if both the resource and the caterpillars (when not starved) have low mortalities, and if caterpillars experience high mortalities earlier in their lives (Stearns 1992). The latter two circumstances apply in the case of *M. rebeli*, whereas the adoption of caterpillars into the same *Myrmica* colony in consecutive years was probably much overestimated (see § 1) in early models of this system (Hochberg *et al.* 1994). Even when consecutive adoptions do occur, the slow developers are at no competitive disadvantage.

Bet hedging is likely to reinforce ergonomic selection. Adults laying a mixture of one- and two-year developing individuals should benefit if occasional catastrophes occur on *M. rebeli* sites or if this spreads the burden of parasitism. Possible catastrophes include years when ruminants eat many or all gentian flowers before or during oviposition (which we have observed twice), reducing *M. rebeli*'s access to the ant resource or eliminating its above-ground population. The specific parasitoid, *Ichneumon eumerus*, which seeks its host in August and September inside *Myrmica schencki* nests, oviposits only in caterpillars larger than *ca.* 10 mg (Thomas & Elmes 1993). This restricts its offspring to fast developers and to slow developers in their second year. By avoiding the parasitoid in the first year, a mixed population of fast and slow developers may experience smaller fluctuations than in simpler host–parasitoid systems.

Whichever factors favour biennialism, it could only evolve if *M. rebeli* possessed a mechanism for remaining attached to its mobile food-source. Our experiments suggest that *M. rebeli* achieves remarkable integration with its host's society, to the extent that the workers select caterpillars in preference to their own larvae when a colony moves (figure 4). Despite this integration, we found no evidence that a third type of *M. rebeli* caterpillar exists, exploiting ants for more than two years. This we consider unlikely to evolve, because caterpillars supplant much of the ant brood, weakening their host colony and making it unlikely to survive as a strong food-source for longer than the average two-year lifespan of the adult worker ants that were present when *M. rebeli* was adopted. Nevertheless, the exploitation of individual *Myrmica* colonies over two years marks yet another contrast to the lifestyle of the predacious *Maculinea*, like *M. arion*, which often exploit two host colonies in a single year (Thomas & Wardlaw 1992).

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