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LETTER

Host propagation permits extreme local adaptation in a social parasite of ants

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Abstract

The Red Data Book hoverfly species *Microdon mutabilis* is an extreme specialist that parasitises ant societies. The flies are locally adapted to a single host, *Formica lemani*, more intimately than was thought possible in host–parasite systems. *Microdon* egg survival plummeted in *F. lemani* colonies > 3 km away from the natal nest, from *c.* 96% to 0% to < 50%, depending on the hoverfly population. This is reflected in the life-time dispersal of females, measured at < 2 m, resulting in oviposition back into the same ant nests for generation after generation. To counter destabilizing effects on the host, *Microdon* manipulates the social dynamics of *F. lemani* by feeding selectively on ant eggs and small larvae, which causes surviving larvae to switch development into queens. Infested colonies rear double the number of new queens, thus propagating the vulnerable local genotype and compensating for damage to the host colonies. The consequences of such extreme host specificity for insect conservation are discussed.

Keywords

Host-parasite interaction, insect conservation, local adaptation, manipulation of ant reproduction, *Microdon mutabilis*, reproductive skew, social parasites.

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INTRODUCTION

Species once regarded as single entities are increasingly shown to be ecologically and genetically diverse, with many displaying local adaptations and some containing cryptic species. Understanding variation within morpho-species is vital for the preservation of genetic diversity and for practical conservation management. Although extreme adaptation is often regarded as an evolutionary dead end, it is unclear at what scale specialization becomes detrimental due to an overdependency on one local resource (Holt & Lawton 1993; Bowers 1999; Greenman & Hudson 2000; Schönrogge *et al.* 2000; Pierce *et al.* 2002). Obligate social parasites provide useful systems to study this question: all are specialists equipped to infiltrate insect societies and exploit the resources inside nests; most are highly localized compared with their hosts; and among the few species studied genetically, the predatory species of *Maculinea* large blue butterfly may consist of multiple cryptic species adapted to different host species (Schönrogge *et al.* 2002; Als *et al.* 2004; Thomas & Settele 2004).

We showed recently that British populations of the hoverfly '*Microdon mutabilis*' consist of two sibling species with overlapping distributions, *M. mutabilis* and *M. myrmicae*, each exploiting a different ant species, *Formica lemani* and *Myrmica scabrinodis* respectively (Schönrogge *et al.* 2002). Both parasites are exceedingly rare compared with their widespread hosts, persisting for many generations on their few known sites. Here we describe much finer-scale evolution, whereby each population of *Microdon mutabilis*

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(*s. str.*) survives only with individual populations or supercolonies of the ant *F. lemani*.

Through coexisting with ants during its entire immature period, *M. mutabilis* is probably more typical of *c.* 10 000 other morpho-species of social parasite than the butterfly genus *Maculinea*, the only such system in which variation in host specificity over distance had previously been explored (Thomas & Settele 2004; Thomas *et al.* 2005). As an adult *M. mutabilis* lives 3–7 days above ground, and females oviposit into the edges of *F. lemani* nests. The larvae then migrate to the inner brood chambers where they live as brood predators for 2 years before pupating in the outer chambers of the nest (Andries 1912; Schönrogge *et al.* 2000).

Infiltrating a host society is the dangerous period in the life cycle of a myrmecophile (Hölldobler & Wilson 1990). In an initial study (Elmes *et al.* 1999), we found that *Microdon* egg mortality from ant attack increased sharply in *F. lemani* colonies over short distances from the mother's natal nest, although the result was inconclusive due to the possible contamination of test eggs through exposure to soil containing chemicals from the maternal ant nest. Here we repeat that trial to eliminate the possible artefact, and replicate it on another site. We hypothesise that such local patterns of egg mortality result in selection for short distance dispersal which should be reflected in the population structure of the hoverfly. Furthermore, if the same individual ant nests are persistently attacked due to local adaptation and low parasite dispersal, we might expect that susceptible types of colony would be outcompeted by more resistant colonies of the same ant species. Here we explore how *Microdon* might evade the danger of extreme specialization to persist, closely coupled with its host, in stable populations. To better interpret *Microdon* biology, we contrast its interaction with ants with new studies of the butterfly *Maculinea arion*, one of the few insect social parasites whose biology is well understood (Thomas & Wardlaw 1990; Schönrogge *et al.* 2000; Thomas & Elmes 2001; Thomas 2002; Thomas *et al.* 2005). Like *M. mutabilis*, *M. arion* is a brood predator in ant colonies; its host is *Myrmica sabuleti*.

MATERIALS AND METHODS

Microdon mutabilis and *Formica lemani* were collected from two populations, on the Isle of Mull, Scotland (NM 518 463 UK grid) and the Burren, Ireland (M2708 Irish grid). That on Mull was typical of the large majority of known *M. mutabilis* populations in being small (estimated < 150 adults), restricted to < 1 ha habitat, and isolated by tens of km from its nearest known neighbouring population. The populations on the Burren occupied the most extensive area of breeding habitat known for this species: numerous patches of limestone pavement across an area of 500 km^2, with many occupied patches situated within 1 km of one another.

Ant colonies were collected under stones and maintained in the laboratory on a diet of *Drosophila* larvae and sugar. *Microdon* was collected in late May either as full-grown larvae or pupae (Schönrogge *et al.* 2000). *Maculinea arion* butterflies were studied on Dartmoor, England and its predacious congeners, *M. nausithous* and *M. teleius* in Savoie, France.

Extreme host-specificity

Eight and six *F. lemani* colonies containing *M. mutabilis* were collected on Mull in 1997 (Elmes *et al.* 1999) and 2001, respectively, and 14 infested colonies on the Burren in 2002. Additionally, two colonies from the Isle of Coll next to Mull were used in the 1997 assays and three colonies from an *F. lemani* population near Limerick (Ireland) were used in 2001. Neither the colonies on Coll or near Limerick showed any sign of *M. mutabilis* activity nor has the syrphid ever been recorded from either location. Distances of < 200 m between colonies were measured by Laser Rangefinder (Impulse), otherwise GPS was used. Laboratory colonies of 100 workers each were established and cultured as in Elmes *et al.* (1999).

Fourteen *M. mutabilis* females from Mull were hatched from pupae that had been isolated from ants for > 3 weeks, and mated with nine males from the same population that had also been hatched in isolation and were available at the same time. No female was mated with more than one male. Mated females were caged individually over soil for oviposition. Unlike our original study (Elmes *et al.* 1999), the soil was not taken from the maternal ant nests; instead, neutral soil was baked at 100 °C for 12 h and re-hydrated with dH_2O to avoid chemical contamination of *Microdon* eggs by ant pheromones, thus avoiding a potential artefact of the 1999 study. Batches of 5–19 sibling eggs were collected and each batch was randomly assigned to a trial colony within 4 h of oviposition, avoiding repeat matches of *Microdon* female and trial colony. As in 1997, the eggs were kept with the ant colonies for 24 h before being scored under a dissecting microscope as either intact or damaged. All eggs defined as 'damaged' quickly died either because their thin shells were torn open by the ants, causing desiccation and collapse, or because they were eaten by the workers. Twenty-four trials were conducted for the 2001 Mull assay and, using the same procedure, 24 females mated by 18 different males from the Burren were used in 43 trials for the 2002 Burren assay. The distances of the natal nests of males and females to the trial colony were used as separate explanatory variables, and the proportion of surviving eggs, excluding the data from naïve populations, was analysed using a generalized linear model with binomial errors and a logit link, testing terms for significance on deletion (Elmes *et al.* 1999).

Genetic analysis of *Microdon mutabilis* population structure

Eighty-one *Microdon* larvae and pupae were collected from *Formica lemani* nests on Mull in May 2001, although except where indicated, we only used nests with three or more individuals, resulting in 69 individuals from 10 nests. All larvae or pupae were transported to CEH Dorset, reared to adults and finally stored at −70 °C before genetic analysis.

DNA extractions

DNA from the heads and upper abdomen (to exclude possible contamination from sperm in mated females) was extracted either by a modified Chelex method (Walsh *et al.* 1991) for microsatellite typing, or a lithium chloride method (Gemmell & Akiyama 1996) for the isolation of microsatellites.

Microsatellite isolation

M. mutabilis is an example of species from which microsatellites are difficult to isolate (Zhang 2004). Microsatellites were enriched independently by two laboratories using three techniques: at CEH Dorset for tetra, tri- and di-nucleotides (Gardner *et al.* 1999; Bond *et al.* 2005), and at Newcastle University (Bioprofiles) (di only) (Hale *et al.* 2001, 2002). Only three scorable (loci that amplified unambiguously and consistently) dinucleotide loci resulted [Bioprofiles: CEH52 (Genebank: DQ146463) F: TGTGCATGAACATTAATTTGCTAAC, R: CCAGAAACGAGAAGAGAAATGG; CEH49 (Genebank: DQ150106) F: TCCCAACAACATTCTCGTCA, R: TCTGATAATCTGCGCTTTGG and from CEH Dorset: Mmut9 (Genebank: DQ146464) F: GCGCATCGTTGAACAC, R: CGTCTTTGGCGTCTGATAA].

Loci were PCR amplified with fluorescently labelled forward primers for 69 flies from 10 nests singularly using Multiplex kit (Qiagen, Hilden, Germany) with an initial 15 min denaturation @ 95 °C, then 32 cycles of 94 °C (30 s), 57 °C (90 s), 72 °C (1 min) with a final extension of 60 °C for 30 min. Products were mixed equally (2.5 μL each) and diluted one-third with sigma water. One microlitre of each dilution was then mixed with 4 μL formamide and 0.17 μL ROX 400 HD (Applied Biosystems, Warrington, UK) size standard per well for electrophoresis on a Basestation (MJ Research, Watertown, MA, USA) using 1.5 μL for 90 min at 40 °C with the supplied KBB buffer system (MJ Research). Results were analysed with Cartographer software (MJ Research) and Mantel tests for isolation by distance were performed with 10 000 randomizations in ZT (Bonnet & Van de Peer 2002; see Appendix 1 for additional details on the loci).

Adult dispersal

Thirty-four *M. mutabilis* (18♀, 16♂) and 29 *M. arion* (18♀, 11♂) were each given unique permanent coloured marks while resting during eclosion above their host ant nests. Their positions were mapped and individual *Microdon* adults were watched continually by JAT and DJS during all periods of activity (typically 8 h day^{-1}), and all movements measured. This was a reliable method for measuring behaviour and dispersal in the main subject of our study, the very sedentary females, but dispersal in > 1-day-old individuals of the more vagile males was probably underestimated. The free-flying, faster, but more conspicuous *Maculinea* were detected by walking throughout the 5 ha study-site (and in neighbouring patches) for 8 h every day for four weeks in two seasons. It was unnecessary to net either species.

Prey-size selection experiments

Microdon mutabilis: Forty-nine 1-year larvae were kept individually and each offered a simultaneous choice of six size-classes of food: 33 ant eggs (0.05 ± 0.02 mg egg^{-1}), four small ant larvae (0.46 ± 0.02 mg each), four large worker larvae (3.48 ± 0.06 mg each), two worker cocoons (6.07 ± 0.15 mg each), two sexual pre-pupae (28.42 ± 0.21 mg each), and two cocoons of gynes or males (31.34 ± 0.27 mg each) over 4 day periods. Pre-dated items were replaced every 24 h. We recorded 67 feeding events by 38 individuals. Food item choice was analysed using Pearson's chi-square. ***Maculinea arion*** was tested in the same way using mid-sized caterpillars (mean weight: 30.4 mg), except that its host *Myrmica sabuleti* brood was classed as five items (eggs, small larvae, large larvae, prepupae and pupae) and choice experiments lasted 56–63 days.

Social manipulation of the host ants

Microdon mutabilis: In 2002, we surveyed 95 *F. lemani* colonies on the Burren (18 with hatched *Microdon* pupae), when sexual and worker brood were in their pupal stages. *Formica lemani* colonies are found under loose stones and the number of adult workers, worker cocoons and sexual cocoons was estimated on a logarithmic scale. Either all or a sample of sexual cocoons were dissected, and the observed sex ratio was applied to the estimates. A generalized linear model with a logit link and binomial errors was used to analyse the worker, male, and gyne brood to adult worker ratios with a binary factor for the presence of *Microdon* as explanatory variable and the number of workers as a co-variable. Significance was assessed by the change of deviance on the deletion of terms. ***Maculinea arion***: 20 *Myrmica* nests containing pupae of the predatory species of *Maculinea* (14 *M. arion*, four *M. nausithous*, two *M. teleius*) were excavated and the contents counted (adult queen, workers, queen and male brood, worker brood) and compared with

24 uninfested nests of the same ant species selected randomly on the same sites. As with *Microdon* (see below), there was no significant difference between the mean size of infested (459 ± 118 workers) and uninfested (392 ± 38 workers) colonies ($t = 0.54$, d.f. = 22, $P = 0.59$).

RESULTS

Extreme host-specificity, dispersal and host-nest faithfulness

Our repeat study of *M. mutabilis* mortality against distance from maternal ant nests, using the same Scottish (Mull) population but with a possible artefact eliminated, produced the same remarkable pattern (Fig. 1a). Egg survival was nearly 100% in *F. lemani* colonies within 100 m of the natal nest but fell abruptly below 50% within 600 m and towards zero in colonies > 3 km away, even though all tests except the furthest (dotted symbols) were bioassays between ant colonies that supported *Microdon* in the field. We obtained a comparable pattern from the Burren, Ireland (Fig. 1b), where *Microdon* populations occur with unusual frequency in patches across 500 km^2. Egg survival fell less steeply with distance in Irish populations, from 95% egg survival in colonies < 50 m from maternal nests to < 50% 20 km away, with the highest mortalities again in distant (50 km), naïve *F. lemani* colonies (Fig. 1b). On both sites, host specificity in *M. mutabilis* appears to be a maternal trait, for the distances to the natal nests of the fathers explained no extra mortality in the bioassays for either region (Mull 2001 $F_{1,21} = 1.05$, $P > 0.3$; Burren $F_{1,40} = 0.42$, $P > 0.5$).

The increase of egg mortality with distance had a parallel in molecular studies of *M. mutabilis* population structure, although not at a scale that exactly corresponded to egg mortality patterns. Although a Mantel test revealed a significant increase in genetic distance with geographic distance, this relationship was entirely due to one nest ($r = 0.54$, $P < 0.001$; Fig. 2 and Appendix 1).

Low dispersal was therefore predicted, and found (Fig. 3). By following adults marked during emergence from ant nests in the Burren, we recorded average dispersal among females of < 1 m from each natal nest during the main oviposition period (days 1–3). Not that the females were inactive. The average total distance moved over 2–3 days was > 20 times further than the distance dispersed, with females walking more often than they flew (70 walks of mean distance 0.14 ± 0.23 m cf. 41 flights of mean distance 0.86 ± 1.5 m). Males, on the other hand, flew more often than they walked (ratio: 1.8 : 1) and travelled longer distances per flight than females (3.82 ± 2.63 m; $P < 0.001$). Dispersal in old males was not recorded, but mature males dispersed *c.* nine times further than the females

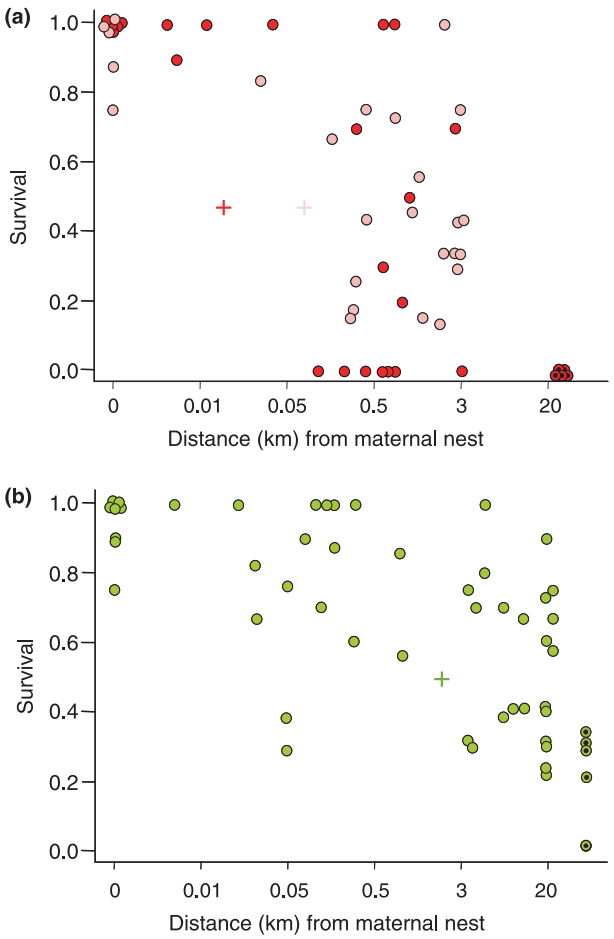

Figure 1 Survival of *Microdon mutabilis* eggs in *Formica lemani* colonies at different distances from the maternal hoverfly's ant nest. (a) Mull, Scotland, a < 1 ha isolated site typical of most *M. mutabilis* populations; red, original 1999 bioassay (Elmes *et al.* 1999) ($F_{1,25} = 28.59$, $P < 0.001$); pink, 2001 bioassay using chemically inert soil ($F_{1,22} = 15.37$, $P < 0.001$). (b) Burren, Ireland, 20 km × 25 km supporting the highest currently known density of *M. mutabilis* populations in the world ($F_{1,41} = 14.79$, $P < 0.001$). In both locations, uniform symbols indicate *F. lemani* colonies containing *Microdon* when sampled; black-centred symbols indicate naïve *F. lemani* colonies from populations unexposed to *Microdon* (not included in the statistical analysis); crosses indicate the distance at which average survival drops to 50%; display of overlapping symbols at 100% and 0% survival enhanced by jitter.

from their natal nests during the first two days (roughly first half) of adult life (males: mean 5.48 ± 2.2 m, maximum 23.05 m dispersed per day; females: 0.62 ± 0.21 m, maximum 2.46 m dispersed per day; $P = 0.05$). All three observations of oviposition were into the outer passages of the mother's natal ant nest (Fig. 3). Barr (unpublished data) observed similar host-colony faithfulness and minimal dispersal by female *Microdon* on Mull. In contrast, *Maculinea*

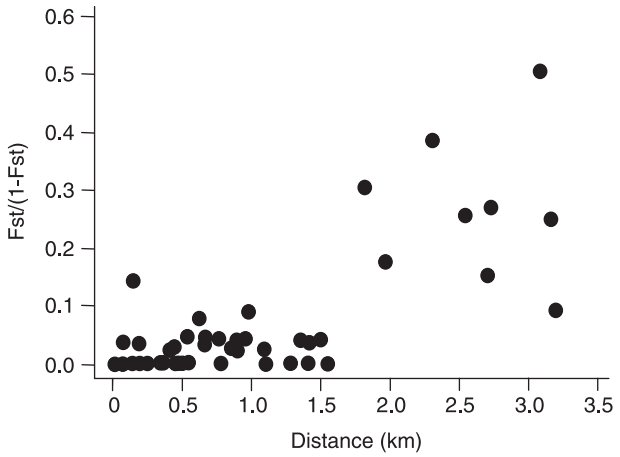

Figure 2 Isolation by distance of the *Microdon mutabilis* 'population' at Mull estimated through microsatellites. Although a Mantel test revealed a significant increase in genetic distance with geographic distance, this relationship was entirely due to one nest that represented all data at distances larger than 1.8 km ($r = 0.54$, $P < 0.001$).

arion females flew indiscriminately within the boundaries of the distribution of their larval resource and oviposited throughout the site (Fig. 3).

A tendency by *Microdon* to oviposit back into maternal ant colonies implies that the same *Formica lemani* nests are parasitized year after year, a hypothesis consistent with infestation patterns in the field. On seven study-sites on the Burren, we found that 9–35% (mean: 22.6 ± 3.3%) of the *Formica* colonies supported *Microdon* in any 1 year, and that the frequency at which marked nests on the Burren were infested (or not) over five successive years differed significantly from that expected by random host selection (Fisher's exact test of fitted Poisson distribution, $P < 0.01$; maximum likelihood of fitting negative binomial frequency, $k = 0.34$, $P > 0.6$). Yet infested nests typically contained a similar number of workers to uninfested ones (551.3 ± 55.1 workers cf. 782.8 ± 108.6 workers, respectively, $F_{1,92} = 2.61$, $P = 0.11$), and showed no apparent difference in their location or surrounding habitat.

Prey-size selection and social manipulation of the host ants

When *M. mutabilis* larvae where offered a choice of different worker brood items, each in abundance, they consumed only eggs, small ant larvae, and on one occasion two large larvae (Fig. 4a; test against equality $\chi^2_3 = 137.2$, $P < 0.001$). We also offered them 768 sexual pre-pupae and pupae, but none was attacked. In contrast, *Maculinea arion* larvae selected to eat the largest available items of *Myrmica sabuleti* ant brood (Fig. 4a; test against equality $\chi^2_3 = 373.3.2$, $P < 0.001$). Unsurprisingly, we found major differences in the type of ant brood surviving under these two systems of social parasitism. By selecting large prey, *Maculinea* larvae kill most of the brood destined to become sexuals, leaving an average of 37 worker, 0.25 male and 0.2 queen pupae per colony, a much lower ratio of sexuals than in uninfested nests (Fig. 4b). With Microdon the opposite occurs: eggs and small ant larvae were killed with such effect that worker production halved ($F_{1,94} = 13.9$, $P < 0.001$), yet we detected no difference in the number of male pupae ($F_{1,44} = 1.32$, $P > 0.05$), and the number of gyne (queen ant) pupae was more than double that in (same-sized) uninfested colonies. This resulted in a sex ratio among sexuals (males : gynes) not different from 0.5 ($F_{1,44} = 4.23$, $P < 0.05$; Fig. 4b).

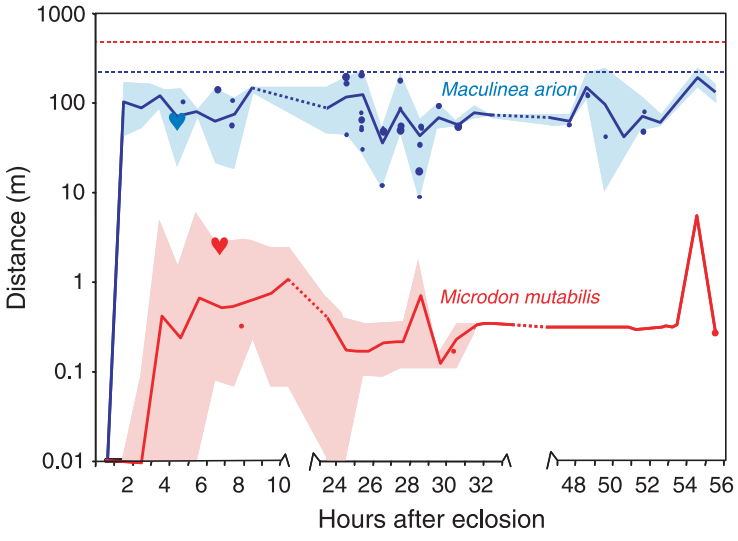

Figure 3 Accumulated distances dispersed from natal ant nests by individual female *Microdon mutabilis* (pink, $n = 18$) and *Maculinea arion* (blue, $n = 18$) marked at eclosion in the Burren, Ireland and Dartmoor respectively. Bold lines indicate the mean distance dispersed by each species from the natal colonies and pale areas the (max–min) range of distances. Dots are observed oviposition events (small, single; medium, 2–3; large > 3); hearts show mating. The dashed lines show the average distance of host ant nests from the boundary of their apparently continuous habitat patches.

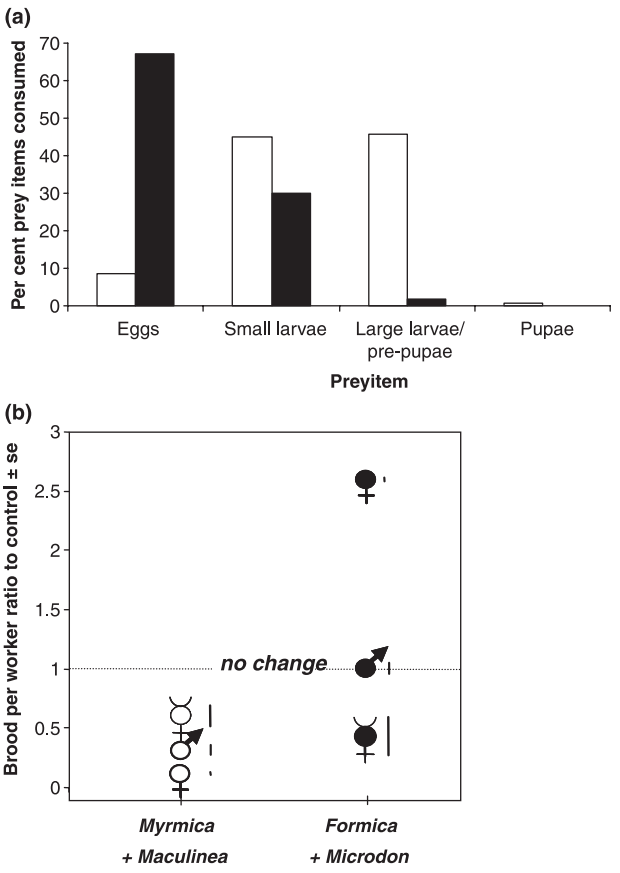

Figure 4 Feeding behaviour and host manipulation by larvae of two types of social parasite. (a) Food choice of *Microdon mutabilis* (black) and *Maculinea arion* (white). (b) Ratio of three types of brood per worker in infested ant nests compared with the number found in un-infested colonies of the same ant species on the same sites. Sexuals: queen pupae (gyne)♀, male pupae; Worker pupae: Vertical lines beside each symbol indicate standard error. Black, *Formica lemani* nests containing *Microdon mutabilis*; White, *Myrmica* species nests containing predatory species of *Maculinea* (*M. arion*, *M. teleius*, *M. nausithous*).

DISCUSSION

This study confirmed Elmes *et al.*'s (1999) suggestion that the *M. mutabilis* populations at Mull show extreme local host specificity. We found a similar (less extreme) pattern in Ireland. Host specificity on such small geographical scales contrasts with that of *Maculinea arion* which, after introduction to vacant UK sites using source populations 1500 km away in Sweden, has survived for 12–22 years with the indigenous *Myrmica sabuleti* host ant colonies, during which it experienced population dynamic interactions indistinguishable from those of the former UK *M. arion* populations (Thomas *et al.* 1998). Two other predacious species of *Maculinea* have also been successfully translocated 900 km from Poland to exploit wild host *Myrmica* populations in the Netherlands (Wynhoff 2001).

In each experiment, *M. mutabilis* egg survival was best described by the distance between test and maternal ant nests, the location of paternal nests explaining no extra mortality. This recalls brood parasitism in the cuckoo *Cuculus canorus*, whose females lay eggs that match a different bird host in different parts of its range, irrespective of the father's origin (Gibbs *et al.* 2000). However, allopatric adaptation in cuckoos birds, like predacious *Maculinea* butterflies (Thomas & Settele 2004), involves switches between different species of host, with each form typically occupying > 1000 km longitude. In *Microdon*, a similar differentiation apparently exists at scales 2–3 orders of magnitude smaller, involving intra-specific adaptation to a single host species' population (Burren) or perhaps supercolony (Mull).

The evolution of small-scale host specificity in *Microdon* is consistent with observed dispersal by females, which was exceptionally low compared with other hoverflies (Wratten *et al.* 2003). Through dispersing as little as 1–2 m from the natal nest, *M. mutabilis* females utilize only a small fraction of the adjacent host ants' habitat, whereas *M. arion*, a comparatively sedentary butterfly species, disperses throughout its habitat patches. Finding significant isolation by distance in *M. mutabilis* across the Mull site is also consistent with limited dispersal, although the relationship depends highly on flies from one colony and *Microdon* population structures need further study. Limited dispersal would be adaptive to the increase in egg mortality, although genetic differentiation in microsatellite markers was found on a slightly larger spatial scale than the egg mortalities. One explanation might be that, like cuckoos (Gibbs *et al.* 2000), sex-linked maternal host specificity in *Microdon* may be detectable only by mtDNA analysis.

The mechanism whereby *M. mutabilis* eggs infiltrate host nests is unknown, but is likely to involve chemical mimicry: while it might not be possible to categorically reject the possibility of environmentally acquired compounds, current evidence strongly suggests that mimetic compounds are inherent rather than acquired (Howard *et al.* 1990a,b; Elmes *et al.* 1999; Napper 2004).

We found 1–36 *Microdon* larvae feeding in individual ant nests, and estimate that an individual larva consumes *c.* 1300 brood items during its 2-year larval stage, roughly equivalent to the production of one ant queen over this period (see Appendix 2; Kipyatkov & Shenderova 1991). Since individual nests are persistently attacked over years, it is unclear how a subset of vulnerable *F. lemani* colonies survive such depletion long enough in < 1 ha (Mull) for *Microdon* first to evolve a colony-specific attribute (e.g. odour) and then to persist. Stable worker numbers may be explained by recruitment from neighbouring nests, a frequent event in

ants such as *F. lemani* and relatives that possess polydomous, polygynous societies, in which congested colonies split and offshoots coalesce with those of well-resourced close relatives or bud into vacant nest sites nearby, to which new queens may later be recruited (Chapuisat & Keller 1999; Brown & Keller 2002). This fails to explain, however, how a vulnerable form of the host ant could persist in the medium term at the scale of a super-colony or population in competition with resistant populations of *F. lemani* whose fitness is undiminished by parasitism. In theory, *Microdon* has evolved further down the dead-end of overspecialization than is usually deemed possible (Wiegmann *et al.* 1993; Pierce *et al.* 2002).

Here we propose a mechanism whereby *Microdon* may circumvent this obstacle by indirectly propagating the genotypes of the individual *F. lemani* colonies that it is able to infest . *M. mutabilis*, like two congeners (van Pelt & van Pelt 1972; Duffield & Thompson 1981), preys only on the eggs or small larvae of *F. lemani*. This is the least efficient way to exploit a host that rears its young in discrete cohorts (Thomas & Wardlaw 1992), and perhaps explains why *Microdon* larvae take 2 years to develop despite living actively at warm temperatures near abundant food for 8 months each year. In contrast *Maculinea arion* feeds on the largest brood in the host colony leaving smaller brood to fatten up before predation (Thomas & Wardlaw 1992). Table 1 summarizes some consequences of these feeding behaviours.

That male brood survival remains unaltered in infested *Formica lemani* nests is explained by *Microdon*'s rejection of large ant brood, but the increased investment in queen brood must result from the manipulation of the worker control over gyne larval development and/or increased food supply to active adult queens. For in un-manipulated ant colonies, the extent to which workers suppress rather than promote potential gyne larvae to develop as workers and not gynes depends (Hölldobler & Wilson 1990) on combinations of a high density of current queens (unaffected by *Microdon*), on high queen productivity (effectively reduced by *Microdon*'s penchant for eggs), and on a low supply of food per larva (much increased in nests containing *Microdon*, since the same adult workforce has fewer than half the number of larvae to feed). By increasing the food flow towards either the remaining large larvae or to adult queens, a larger proportion of queen potential larvae are expected to develop as sexuals (Hölldobler & Wilson 1990).

Table 1 Prey-size selection and its consequences in two predatory myrmecophiles *Maculinea arion* and *Microdon mutabilis*

Maculinea arion	*Microdon mutabilis*
Food selection	
Large ant brood	Small ant brood
Impact on ant colony	
58% brood eaten	53% brood eaten
92% gynes eaten	Queen brood doubles
Costs to social parasite	
Low survival with host ant	Inefficient feeding
	2-year development
	Narrow host range
Benefits to social parasite	
Efficient feeding	Promotes host genotype
Wider host range	
Usually 1 year development	

Here perhaps is a mechanism to avoid over-specializing towards local extinction (Wiegmann *et al.* 1993; Pierce *et al.* 2002), through the propagation – and potential export – of the vulnerable genotype(s) within a host population. To further understand the implications of local adaptations at such small scales, questions about the fate of gynes produced in infested colonies, and the longer term dynamics of such colonies within the population, need to be addressed.

With data from only two regions, we can merely speculate whether *M. mutabilis* has experienced the 'extraordinary radiation' (Wiegmann *et al.* 1993) predicted of extreme specialists across its global range from Ireland to Japan. We tentatively suggest that it may, and that this hoverfly may have (co-)evolved into mutually incompatible forms, each adapted to a single host species' population (Burren) or perhaps super-colony (Mull). Among the 10 000 other morpho-species of social parasite (including *c.* 350 known *Microdon* species) estimated to exist (Elmes 1996; Schönrogge *et al.* 2002), ecological specificity has been studied only in five *Maculinea* species (Thomas *et al.* 2005). *Maculinea* life-styles are atypical due to their exploitation of ants in just the final larval instar; nevertheless, molecular studies of its predatory 'species' suggest multiple cryptic speciation across the Palaearctic (Als *et al.* 2004; Thomas & Settele 2004). If *M. mutabilis* is the paradigm, substantially greater local specialization is expected within other social parasites, several of which (like *M. mutabilis*) are already Red Data listed. Clearly, the conservation problem will be amplified if individual populations within a morpho-species' range prove to be functionally unique forms or cryptic species.

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REFERENCES

Als, T.D., Vila, R., Kandul, N.P., Nash, D.R., Yen, S.H., Hsu, Y.F. *et al.* (2004). The evolution of alternative parasitic life histories in large blue butterflies. *Nature*, 432, 386–390.

Andries, M. (1912). Zur Systematik, Biologie, und Entwicklung von Microdon Meigen. *Zeit. f. Wiss. Zool.*, 103, 300–361.

Bond, J.M., Porteous, R., Hughes, S., Mogg, R.J., Gardner, M.G. & Reading, C.J. (2005). Polymorphic microsatellite markers, isolated using a simple enrichment procedure, in the threatened smooth snake (*Coronella austriaca*). *Mol. Ecol. Notes*, 5, 42–44.

Bonnet, E. & Van de Peer, Y. (2002). ZT: a software tool for simple and partial Mantel tests. *J. Stat. Softw.*, 7, 1–12.

Bowers, R.G. (1999). A baseline model for the apparent competition between many host strains: the evolution of host resistance to microparasites. *J. Theor. Biol.*, 200, 65–75.

Brown, W.D. & Keller, L. (2002). Queen recruitment and split sex ratios in polygynous colonies of the ant *Formica exsecta*. *Ecol. Lett.*, 5, 102–109.

Chapuisat, M. & Keller, L. (1999). Extended family structure in the ant *Formica paralugubris*: the role of the breeding system. *Behav. Ecol. Sociobiol.*, 46, 405–412.

Duffield, R.M. & Thompson, F.C. (1981). Biology of *Microdon fuscipennis* (Diptera, Syrphidae) with interpretations of the reproductive strategies of *Microdon* species found north of Mexico. Tables 2 & 3 in Duffield, R. M. 1981. Biology of *Microdon fuscipennis* (Diptera: Syrphidae) with interpretation of the reproductive strategies of *Microdon* species found north of Mexico. *Proc. Entomol. Soc. Wash.*, 83, 716–724.

Elmes, G.W. (1996). Biodiversity research and its perspectives in the east Asia: biological diversity of ants and their role in ecosystem function. In: *Meeting on Biodiversity Research and its Perspectives in the East Asia* (eds Byung-Hoon, L., Tae-Heung, K. & Byung-Yun, S.). Korean Institute for Biodiversity Research (KIBIO), Chonbuk National University, Chonju, pp. 33–48.

Elmes, G.W., Barr, B., Thomas, J.A. & Clarke, R.T. (1999). Extreme host specificity by *Microdon mutabilis* (Diptera: Syrphidae), a social parasite of ants. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 266, 447–453.

Gardner, M.G., Cooper, S.J.B., Bull, C.M. & Grant, W.N. (1999). Isolation of microsatellite loci from a social lizard, *Egernia stokesii*, using a modified enrichment procedure. *J. Hered.*, 90, 301–304.

Gemmell, N.J. & Akiyama, S. (1996). An efficient method for the extraction of DNA from vertebrate tissues. *Trends Genet.*, 12, 338–339.

Gibbs, H.L., Sorenson, M.D., Marchetti, K., Brooke, M.d.L., Davies, N.B. & Nakamura, H. (2000). Genetic evidence for female host-specific races of the common cuckoo. *Nature*, 407, 183–186.

Greenman, J.V. & Hudson, P.J. (2000). Parasite mediated and direct competition in a two host shared macroparasite system. *Theor. Popul. Biol.*, 57, 13–34.

Hale, M.L., Bevan, R. & Wolff, K. (2001). New polymorphic microsatellite markers for the red squirrel (*Sciurus vulgaris*) and their applicability to the grey squirrel (*S. carolinensis*). *Mol. Ecol. Notes*, 1, 47–49.

Hale, M.L., Squirrell, J., Borland, A.M. & Wolff, K. (2002). Isolation of polymorphic microsatellite loci in the genus *Clusia* (Clusiaceae). *Mol. Ecol. Notes*, 2, 506–508.

Hölldobler, B. & Wilson, E.O. (1990). *The Ants*. Springer Verlag, Berlin.

Holt, R.D. & Lawton, J.H. (1993). Apparent competition and enemy free space in insect host parasitoid communities. *Am. Nat.*, 142, 623–645.

Howard, R.W., Akre, R.D. & Garnett, W.B. (1990a). Chemical mimicry in an obligate predator of Carpenter Ants (Hymenoptera, Formicidae). *Ann. Entomol. Soc. Am.*, 83, 607–616.

Howard, R.W., Stanley-Samuelson, D.W. & Akre, R.D. (1990b). Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera, Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera, Formicidae). *J. Kansas Entomol. Soc.*, 63, 437–443.

Kipyatkov, V.E. & Shenderova, S.S. (1991). Effects of temperature and photoperiod on egg laying and productivity of queens of ants (Hymenoptera, Formicidae, *Formica rufa* L. Group). *Entomol. Oboz.*, 1, 36–46.

Napper, E.K.V. (2004). *Chemical and Behavioural Interactions Between Ants and Microdon* Hoverflies. University of Southampton, Southampton, UK.

van Pelt, A.F. & van Pelt, S.S. (1972). *Microdon* (Diptera: Syrphidae) in nests of *Monomorium* (Hymenoptera: Formicidae) in Texas. *Ann. Entomol. Soc. Am.*, 65, 977–979.

Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B. *et al.* (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annu. Rev. Entomol.*, 47, 733–771.

Schönrogge, K., Wardlaw, J.C., Thomas, J.A. & Elmes, G.W. (2000). Polymorphic growth rates in myrmecophilous insects. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 267, 771–777.

Schönrogge, K., Barr, B., Wardlaw, J.C., Napper, E., Gardner, M.G., Breen, J. *et al.* (2002). When rare species become endangered: cryptic speciation in myrmecophilous hoverflies. *Biol. J. Linnean Soc.*, 75, 291–300.

Thomas, J.A. (2002). Larval niche selection and evening exposure enhance adoption of a predacious social parasite, *Maculinea arion* (large blue butterfly), by *Myrmica* ants. *Oecologia*, 132, 531–537.

Thomas, J.A. & Elmes, G.W. (2001). Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus Maculinea. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 268, 471–477.

Thomas, J.A. & Settele, J. (2004). Evolutionary biology – butterfly mimics of ants. *Nature*, 432, 283–284.

Thomas, J.A. & Wardlaw, J.C. (1990). The effect of queen ants on the survival of *Maculinea arion* larvae in *Myrmica* ant nests. *Oecologia*, 85, 87–91.

Thomas, J.A. & Wardlaw, J.C. (1992). The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. *Oecologia*, 91, 101–109.

Thomas, J.A., Clarke, R.T., Elmes, G.W. & Hochberg, M.E. (1998). Population dynamics in the genus *Maculinea* (Lepidoptera: Lycaenidae). In: *Insect Population Dynamics: in Theory and Practise* (eds Dempster, J.P. & McLean, I.F.G.). Chapman & Hall, London, pp. 261–290.

Thomas, J.A., Schönrogge, K. & Elmes, G.W. (2005). Specializations and host associations of social parasites of ants. In: *Insect Evolutionary Ecology* (eds Fellowes, M.D.E., Holloway, G.J. & Rolff, J.). CABI Publishing, Wallingford, UK, pp. 479–518.

Walsh, P.S., Metzger, D. & Higuchi, R. (1991). Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques*, 10, 506–513.

Wiegmann, B.M., Mitter, C. & Farrell, B. (1993). Diversification of carnivorous parasitic insects - extraordinary radiation or specialized dead-end. *Am. Nat.*, 142, 737–754.

Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R. & Tylianakis, J.M. (2003). Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia*, 134, 605–611.

Wynhoff, I. (2001). *At home on foreign meadows: the reintroduction of two Maculinea* butterfly species. Wageningen Agricultural University, Wageningen, Netherlands.

Zhang, D.X. (2004). Lepidopteran microsatellite DNA: redundant but promising. *Trends Ecol. Evol.*, 19, 507–509.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from http://www.blackwell-synergy.com:

Table S1 *Microdon mutabilis* microsatellite allele frequencies for Mull nests.

Table S2 *Microdon mutabilis* microsatellite allele frequencies for all sites.

Appendix S1 *Microdon mutabilis* microsatellite loci.

Appendix S2 The impact of *M. mutabilis* on host ant colonies.

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