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PARENTAL CARE IN THE SUBSOCIAL INTERTIDAL BEETLE, BLEDIUS SPECTABILIS, IN RELATION TO PARASITISM BY THE ICHNEUMONID WASP, BARYCNEMIS BLEDIATOR

by

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(With 4 Figures)
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Introduction

The great majority of insects do not invest in their young after birth. The occurrence of parental care in insects is therefore of considerable interest and several hypotheses have been put forward to account for the sporadic evolution of this life-history trait. Two factors have been suggested to be of particular importance in the evolution of parental care in insects: protection against a harsh environment, and protection against parasites and predators (*e.g.* Wilson, 1971; Eickwort, 1981; Tallamy & Wood, 1986; Wyatt, 1987). The saltmarsh staphylinid beetle *Bledius spectabilis* is of peculiar interest because there is evidence that parental care is important in relation to both physical and biotic environmental factors. Wyatt (1986) provided experimental confirmation of Larsen's (1936; 1952) suggestion that a major benefit of parental care in *Bledius spectabilis* is the protection of the young from the adverse effects of the tide. By appropriate burrow design and her patrolling behaviour, the mother beetle keeps her eggs and young larvae free from flooding and anoxia (Wyatt, 1986). However, in addition there is experimental evidence that the mother also protects her young against predation by the carabid beetle *Dicheirotrichus gustavi* Crotch (Wyatt & Foster, in press).

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The other important biological factor that might be important in the evolution of parental care is the protection of the young against parasitoid attack. However, there are relatively few experimental studies of parasitism in relation to parental care in insects. RALSTON (1977) showed that egg clusters of tropical reduviid bug (*Zelus* sp.) suffered significantly more parasitism when the guarding male was removed. In an interesting recent study of the webspinner *Clothoda urichi* (Saussure) (Embioptera), EDGERLY (1987, 1988) showed that the female protects her young by physically repelling egg parasites (scelionids) and by producing a substantial covering for her egg masses. There is experimental evidence that several of the non-eusocial aculeate Hymenoptera protect their young against parasitoids and brood parasites (*e.g.* SAKAGAMI & MAETA, 1977; PECKHAM, 1977; ABRAMS & EICKWORT, 1981; EVANS & HOOK, 1982a, b).

Is protection against parasitoids important in the evolution of parental care in *Bledius spectabilis*? Previous accounts of *Bledius* have not mentioned parasitoids (LARSEN, 1936, 1953; WOHLENBERG, 1937; WINGERDEN *et al.*, 1981). We were therefore excited to discover large numbers of the parasitic wasp *Barycnemis blediator* (Hymenoptera: Ichneumonidae: Tersilochinae) among the *Bledius* aggregations on Scolt Head Island. *Barycnemis* is widely distributed, but nothing is known of its biology: AUBERT (1970) describes it from Roscoff (Finistere, France), and HORSTMANN (1980) reports it in northern Germany and Holland. This is its first recording from Britain: we have found it in Pembrokeshire (Wales) as well as in Norfolk.

We describe here the behaviour of the wasp and its possible effects on the beetle populations. Very few previous studies on subsocial behaviour have combined experimental observations with a life-table analysis of the net effect of this behaviour on the host population. TALLAMY & DENNO (1981a, b; 1982) studied the effect of parental care in relation to predation and its effects on survivorship in the lace-bug *Gargaphia solani* (Hemiptera: Tingidae). *Bledius spectabilis* presents an excellent opportunity for studying the importance of parental care in relation to parasitoid attack, because we can combine an experimental study of parasitism with a detailed account of the life-table of the beetle populations (see WYATT, 1984). This life-table analysis showed that most of the mortality occurs in the period just after the larvae leave the maternal burrow about two-thirds of the way through the first instar. In addition, it was established that parasitism was an important cause of mortality in the third instar.

In this paper, we describe the basic biology and host-finding behaviour of *Barycnemis blediator* and ask the following questions. How important is the wasp in the life of the beetle? Does the mother beetle protect the young from parasitic attack? Which life-history stages are most vulnerable to wasp attack? Is parental care more important in protecting the young against the tides, against predators or against parasitoids?

Methods

Study site.

Field observations were made in 1979-1981 on Missel Marsh at Scolt Head Island NNR on the North Norfolk coast, U.K. (grid ref: TF 815462). A map of the area and a description of the general saltmarsh habitat are given by FOSTER & TREHERNE (1975). *Bledius spectabilis* populations were confined to a narrow band 0.8-1.55 m above Ordnance Datum (O.D.), along the banks of the saltmarsh creeks at the level of the *Salicornietum* (*sensu* Beeftink, 1977) (see WYATT & FOSTER, 1988).

Field observations.

Individual female *Barycnemis* were followed as they searched on the marsh surface within *Bledius* aggregations. The wasp's behaviour at each heap of *Bledius* tailings was noted and timed. After the wasp had moved away, the heap was marked for later investigation. Care was taken not to trample the habitat. Later, but before the next tide washed away the heaps, each burrow was traced and dug up to find the insect within (see WYATT (1986) for method used).

To assess the effect of the tides on the parasitoid populations, we made ten sweeps—one per stride—of a sweep net over a large *Bledius* aggregation each morning at 1100 hours for 3 days before and 2 days after the first covering tide following a period of neap tides (4-8 July, 1979). The sweeps covered the same areas each day. The wasps were released *in situ* after sampling. To observe the reaction of adult *Barycnemis* to the incoming tide, we released the parasitoids from glass vials onto *Salicornia* plants in isolated habitat portions. We observed the wasp as the tide surrounded and then covered the plants and habitat. Wasps were also followed as they searched for heaps during the time just before the arrival of the tide.

Field arena experiments.

In order to assess the behaviour and performance of the parasitoids under more controlled conditions, we established, in the middle of the *Bledius* aggregations, experimental "arenas" containing *Bledius* of known age (Fig. 1). A core of beetle-free mud, 20 cm deep and 15 cm in diameter, was placed in a protective rigid plastic sleeve. A *Bledius* larva was placed in each of twenty holes, 30 mm deep and 3 mm in diameter, made in the top of the core. A small plastic ring placed around each hole prevented the animal from escaping until it had established itself in the hole. Each hole was marked with a flag. Within about an hour, each animal produced tailings at the entrance to its hole. When all the larvae had become established in their new holes, the arena, in its protective sleeve, was placed flush with the marsh surface in a 15-cm diameter hole dug with a corer in the middle of a *Bledius* aggregation (Fig. 1). The join between the arena and the marsh was smoothed over and the small ring around each burrow was removed. Female wasps searching the habitat walked on and off the arena without hesitation, apparently not distinguishing it from the rest of the saltmarsh surface. The wasps climbed up the flags, treating them as *Salicornia* plants. At the end of the experiment, each burrow was checked

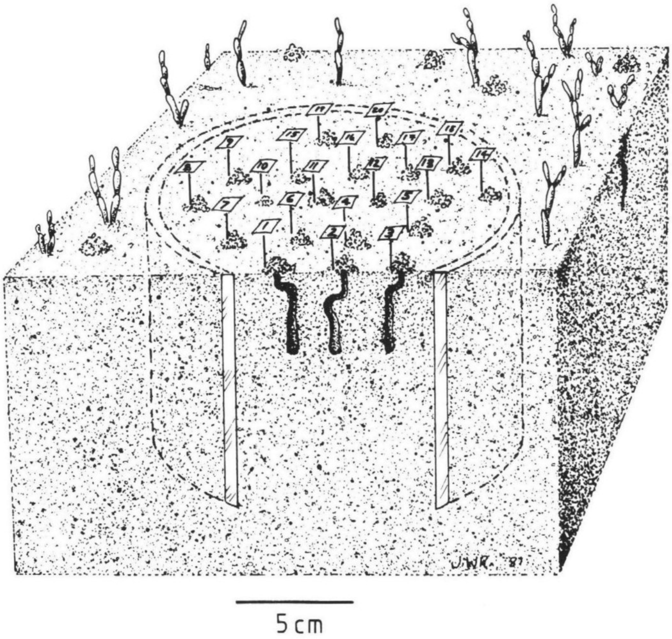

Fig. 1. Diagram of the arena used in field experiments on parasitism. In a *Bledius spectabilis* aggregation on Scolt Head Island, a core of the habitat (20 cm deep, 15 cm diameter) was removed and replaced with a core of mud, held in a protective rigid plastic sleeve, which contained a number of beetle larvae of known age in individual burrows. Each burrow was marked with a flag. The wasps walked naturally onto the arena from surrounding areas. The behaviour of the wasps at each burrow was observed and the success of parasitism was established by digging up the burrows and dissecting the larvae at the end of the experiment. See text for further details.

to confirm that the animal in the burrow was the same as at the beginning of the experiment.

For experiments on the success rate of *Barycnemis* with *Bledius* larvae of different ages, the *Bledius* larvae were reared from eggs in the laboratory to the required stage, which ensured that they had not had any previous contact with *Barycnemis*. Only one attempt by a wasp was allowed for each larva. At the end of the experiment, the larvae were dissected to find what proportion had been parasitized.

Except where otherwise stated, values are given as means ± S.E. (N).

Results

General biology of *Barycnemis blediator*.

Adult *Barycnemis* were active on the marsh surface within *Bledius* aggregations during both day and night, from June to August, the period when *Bledius* larvae are available for parasitization (Wyatt, 1984). In 1981, a total of 64 ± 24 (15) *Barycnemis* adults emerged per m^2 of *Bledius* aggregation during these months. This figure was estimated from the difference between the number of wasp pupae containing pharate adults at the beginning and end of the summer (see WYATT, 1984). The wasps were very widely dispersed over Scolt Head: *Barycnemis* pupae were found even in small isolated *Bledius* aggregations, less than 0.5 m^2 in area, far from the main *Bledius* areas (see WYATT & FOSTER, 1988).

The pearly white eggs of *Barycnemis* are kidney-shaped ovoids $0.78 \pm 0.005 \times 0.21 \pm 0.005$ mm (17). The wasp laid the egg in the haemocoel of the host larva. Of 56 *Bledius* larvae dissected just after parasitization, in 54% the egg was placed in the thorax, in 36% in the abdomen, and in 10% at the back of the head. The wasp egg hatched between 30 and 50 h after oviposition in the host (at about 16°C). The first instar wasp larva was 0.1 × 0.8 mm when it hatched and at pupation the wasp had grown to 2.0 × 4.0 mm.

Effect of the tides on *Barycnemis blediator*.

The larva of *Barycnemis* lives within the *Bledius* larva and is therefore protected from the tide by the behaviour of its host. The wasp larva does not emerge from its host until the very end of the last *Bledius* instar, by which time the beetle larva has constructed the water-resisting pupal chamber (LARSEN, 1950; WYATT, 1984). The wasp pupa is thus protected from the tide throughout its long overwintering stage by the structure built by its host.

However, the effect of the tides on the adult wasps is very marked. The wasps are abundant on the marsh surface during periods of neap tides, but virtually disappear after the first tide has covered the marsh (Fig. 2). These sweep-netting observations were confirmed by a close search of the habitat for the wasps: they had not just flown away to higher ground but had disappeared altogether. Seven hours separated the tide's ebb and the sample at 1100 hours on July 7, but the wasps had still not returned.

Observations on *Barycnemis* adults active on the saltmarsh as a covering tide submerged the habitat revealed that the majority (19/25) of the wasps were simply washed away as the water gently covered the marsh. Three wasps attempted to fly from a *Salicornia* plant tip as the water reached them, but less than 50 cm from the plant, they fell into the water and, helpless, were carried away. Three wasps were seen to fly very weakly away from the immediate habitat. Thus, even on a calm day, almost 90% of the wasps were observed to be washed away by the tide.

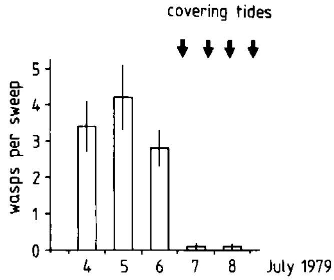

Fig. 2. The density of adult *Barycnemis blediator* on the marsh surface on 3 days before and 2 days after the first tide to cover the *Bledius* zone following a period of non-submerging, neap tides. Each histogram is the mean (± S.E.M.) of 10 standard sweeps over the *Bledius* zone taken at 11.00 h. The arrows indicate the times of the submerging high tides.

The wasps appeared to make no attempt at all to escape from the tide. It is possible that some of the wasps survived the tidal immersion, but adult wasps did not reappear in any numbers during the period of covering tides. The wasps that did appear at low tide during these periods had probably eclosed in the short time since the previous high tide. Numbers did not build up each day as they did during the neaps, because each day's eclosion was washed away by the next tide.

Host-searching behaviour by *Barycnemis*.

The female *Barycnemis blediator* walked rapidly over the marsh surface and investigated heaps of beetle tailings with its antennae. After touching the heap with its antennae, the wasp either left and continued its search or, curving its abdomen forward under the thorax, probed the tailings with its extended ovipositor to find the burrow entrance under the tailings (Fig. 3). When an artificial circular groove was made under tailings, the wasp would follow the groove and go round in circles many times before giving up. At some natural *Bledius* heaps, the wasp also gave up, after up to 30 s, before it had found the burrow. The stimulus to probe with the ovipositor was contained in the tailings—some isolated lumps of tailings prompted the wasp to probe. Having located the burrow, the wasp arched its wings up above its body and, ovipositor first, it disappeared down the burrow. Below ground the wasp attempted to paralyze the larva and lay an egg in its haemocoel.

The wasp reappeared above ground after between 5-240 s (mean 67 ± 4(74)). We were unable to deduce from the wasp's behaviour on the

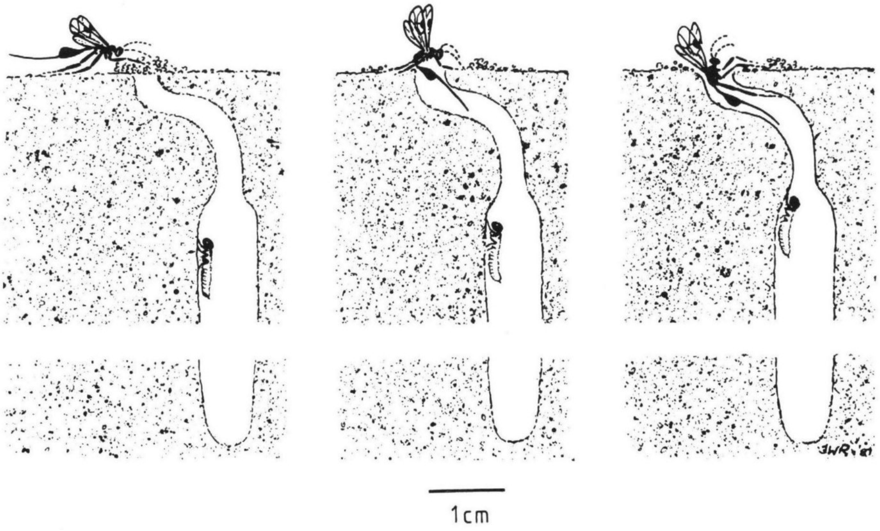

Fig. 3. Diagrams of the sequence of behaviour of *Barycnemis blediator* at the entrance to a *Bledius* burrow. The wasp a) antennates the heap of beetle tailings, b) probes with her ovipositor for the burrow opening under the tailings, and c) with her wings raised up and forwards, goes down the burrow, ovipositor first.

heap whether or not it had been successful. The wasp remained on the heap for a short time (7.7 ± 0.8 s (22)) before moving off and continuing the search. On many occasions, the wasp appeared to smear the heap with its ovipositor: this may have been some form of ''marking'' behaviour. A wasp female did not go down recently visited burrows a second time, whether or not she had been successful on the first visit. Out of 22 occasions that a wasp investigated a heap above a burrow she had previously gone down within one hour, on 19 she immediately rejected the heap and moved on, and on 3 she probed with her ovipositor before rejecting the heap. However, other *Barycnemis* females were observed to go down a burrow previously visited by another female ($n = 14$). It is possible that the first wasp had been unable to parasitize the beetle larva (see Table 2). Beetle larvae containing more than one wasp were only very rarely observed: among more than 2000 parasitized *Bledius* larvae dissected, none contained more than one *Barycnemis* larva, only one had two eggs, and only one other had an egg and a *Barycnemis* larva.

Large areas of saltmarsh were searched by each wasp. For example, during 99 minutes of observation, one wasp investigated 62 heaps of

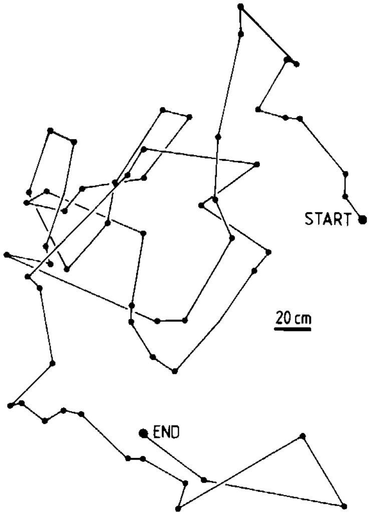

Fig. 4. The path taken by a female *Barycnemis blediator* investigating heaps of beetle tailings (filled circles) on Missel Marsh, Scolt Head Island, 25 June 1979. The wasp was followed for 99 minutes.

beetle tailings within an area of 1.3 m^{-2} (Fig. 4). The direct path taken between the heaps investigated was a total of 18.6 m.

Selection of *Bledius* burrows by *Barycnemis*.

Field observations showed that, although the wasps investigated any heap of tailings, they only went down those burrows that contained a *Bledius* larva alone after dispersal (with one exception in 132 observations) (Table 1). They rejected burrows belonging to other species, such as *Heterocerus fossor* Kiesenwetter (at any stage of their life-cycle), adult male *Bledius*, and maternal burrows containing eggs and mother *Bledius*. The wasp was significantly more likely to go down the individual burrows of post-dispersal first instar larvae than the maternal burrows containing mothers and first instar larvae (Table 1).

One might have expected that a maternal burrow, containing on average 2.8 ± 0.4 (32) larvae, would be more attractive than a burrow containing one *Bledius* larva alone. However, although the wasps often started to probe above maternal burrows with *Bledius* larvae, they did not—with one exception—go down these burrows (Table 1). A possible explanation for this is that young first instars are not attractive to the

TABLE 1. The behaviour of *Barycnemis blediator* females on heaps of tailings of *Bledius spectabilis* under natural conditions

	Reject	Probe then reject	Down
Bledius			
Male	**2**	**0**	0
Female alone	**1**	**0**	0
Female + eggs	**10**	**0**	0
Female + eggs + larvae*	**11**	**3**	1
1st instar larvae alone*	**27**	**14**	41
2nd + 3rd instar larvae	**10**	**1**	5
Heterocerus fossor			
Adult	**3**	**0**	0
Larva	2	2	0

Observations from following five wasps in June 1979, 1980, and 1981 on Missel Marsh, Scolt Head Island. Reject = the wasp left the heap within 1-3 secs. PROBE THEN REJECT = the wasp probed the tailings with her ovipositor before rejecting the heap and continuing searching. Down = the wasp went down the burrow under the heap. The null hypothesis that a female wasp was equally likely to go down a burrow occupied by a first instar larva alone after dispersal as a maternal burrow containing an adult *Bledius* and larvae (lines 4 and 5*) was rejected (χ^2 with continuity factor = 7.8, $p<0.05$, d.f. = 1). The small number of second and third instar larvae reflects the early stage of the season.

wasp. To test this, we took young first instar larvae from maternal burrows and placed them singly in holes in an arena (see Methods, Fig. 1). The wasps went down 45 burrows containing a larva taken from a maternal burrow. It might also have been argued that, although a wasp would go down a burrow containing a young larva from a maternal burrow, it would not actually lay an egg in a larva so young. However, 92% of the 25 larvae dissected after the arena experiment had been parasitized by the wasp that had gone down their burrow. Moreover, the eggs hatched and developed normally in these larvae; even larvae that were only 2-3 days old were able to support the burden of a wasp larva.

Success rate of parasitization by *Barycnemis*.

Our field observations established that *Barycnemis* would go down the individual burrows of all 3 larval instars of *Bledius* (Table 1). However, the success rate of the wasp per visit down a burrow could not be found by dissecting larvae collected in the field, because they might already have been parasitized. Therefore, we measured the success rate of wasps in arena experiments in the field using laboratory-reared, parasite-free

TABLE 2. The success rate of *Barycnemis blediator* in artificial arenas in the field

Instar	Parasitized	Not parasitized	% Parasitized
1st	31	2	94
2nd	9	4	69
3rd	8	15	35

Experiments carried out on Missel Marsh, Scolt Head Island, 15 July 1981. The number of *Bledius spectabilis* larvae of different instars parasitized in a single attempt per larva was recorded. The beetle larvae had been reared in the laboratory to prevent prior contact with the wasp. The first instar larvae were of post-dispersal size. The null hypothesis that there was no difference between instars in the proportion parasitized per visit by *Barycnemis* was rejected ($\chi^2 = 22.4$, $p < 0.001$, d.f. = 2). The difference between the success rate with first and second instars was not significant (χ^2, with continuity factor = 3.1, $p > 0.05$, d.f. = 1).

TABLE 3. The time in seconds spent by *Barycnemis blediator* down burrows of different *Bledius spectabilis* instars

Instar	Time spent down burrow(s) (All observations)	Time spent down burrow(s) parasitized	Time spent down burrow(s) not parasitized
1st	61 ± 4 (33)	62 ± 4 (31)	49 ± 6 (2)
2nd	67 ± 6 (18)	72 ± 7 (13)	55 ± 13 (5)
3rd	76 ± 10 (23)	91 ± 18 (10)	64 ± 16 (13)

Values are means ± S.E.M. (n). There was no significant difference between the time spent down the burrows of the three different instars (Column 1) (ANOVA: F = 0.994, p = 0.38, d.f. = 2). The time spent down a burrow successfully (Column 2) or unsuccessfully (Column 3) parasitizing a larva was not significantly different (t test: 2nd instar, p = 0.2; 3rd instar, p = 0.3).

TABLE 4. Field levels of parasitism of *Bledius spectabilis* by *Barycnemis blediator* at Scolt Head Island

Instar	No. of larvae parasitized	Total no. of larvae dissected	% Parasitized	% Parasitized during the instar
1st in maternal burrow)	0	500	0	0
1st (after dispersal)	6	546	1.1	1.1
2nd	12	217	5.5	4.4
3rd	60	413	14.5	9.0

Data from dissection of 5 sample cores collected on each of 8 sampling occasions between June and September 1981. The percentage of larvae parasitized by the wasp during each instar was calculated by subtracting the level of parasitism in the previous instar.

larvae (Table 2). These experiments showed that that rate of success per burrow visit by *Barycnemis* was much greater with first instar *Bledius* larvae than with older instars (Table 2).

Our observations also showed that the time spent by the wasp down the burrows did not vary significantly with the age of the *Bledius* larvae (Table 3). In addition, the time spent down the burrow was not significantly influenced by whether the parasitism was a success or a failure (Table 3).

Levels of parasitism in the field.

Field levels of parasitism by *Barycnemis* were found by dissecting all the larvae from a sample of 5 cores for each of eight sampling dates during the summer (June to September) of 1981 (Table 4). The cores were carefully picked through so that the first larvae in maternal burrows could be distinguished from first instar larvae in individual burrows after dispersal.

Discussion

Our observations show that the mother *Bledius* plays a vital role in the protection of her young larvae against parasitism by the ichneumonid wasp *Barycnemis blediator.* Life-table analysis and population sampling showed that the wasp is an important natural enemy of the beetle: the wasp occurs at high densities (up to 100 coccoons m^{-2} have been recorded), it is very widely distributed, up to 15% of the immature stages are killed by the wasp, and the adult wasps are active on the marsh surface throughout the period when the beetle larvae are developing. Only once in 132 observations did a wasp go down a burrow containing a female and larvae: all the other burrows that we saw the wasp go down contained individual, post-dispersal *Bledius* larvae. None of the 500 dissected 1st instar larvae collected from maternal burrows had been parasitized (Table 4). This was *not* because 1st instars in maternal burrows were in some way unattractive or unsuitable for the wasps: field experiments showed that wasps were highly successful in parasitizing larvae taken from maternal burrows and placed in individual experimental burrows. By far the most plausible explanation why the wasps did not go down maternal burrows is because they were in some way deterred by the presence of the mother beetle.

When the *Bledius* larvae hatch from the eggs laid around the central burrow, they remain in the living chamber of the maternal burrow, where up to seven larvae may be found at any one time. Such a concentration of vulnerable first instar larvae would be a bonanza for a parasitoid wasp if the burrow were not guarded. The *Bledius* adults prevent such opportunism: all intruding animals, including conspecifics, predators and parasites, are successfully repulsed from the burrow. Indeed, it appears that *Barycnemis* does not normally attempt to go down maternal burrows, despite the potential reward: perhaps because the likelihood of injury inflicted by the *Bledius* adult has selected against this behaviour.

We established that the 1st instars, which spend about 60% of their life in the maternal burrow, are particularly susceptible to parasitism. Arena experiments in the field, using larvae reared in the laboratory, showed that the success rate of the wasp was much higher with 1st instars (94%) than with 2nd (69%) or 3rd (35%) instars (Table 2). The period spent in the maternal burrow is therefore particularly important in relation to parasitism, because this is the age when the larvae are maximally susceptible to the wasp. The probability or "risk" of parasitism during a particular period will be proportional to the duration of that period multiplied by the chance of success of each wasp visit during that period. Thus, although the individual 1st instars are likely to be parasitized by almost every wasp that visits them, the overall "risk" during this stage is fairly low, because the stage itself is short. Table 5 lists the risks of parasitism for each larval stage of *Bledius*. It will be seen that the period of 8 days spent in the maternal burrow reduces the total risk of parasitism by almost a quarter (24%).

The observed field levels of parasitism of each instar are not quite in line with the predictions of risk, based on stage duration and susceptibility. Table 5 shows that the risk of parasitism for the three instars should be in the ratio 1:1.6:1.8, whereas the observed rates of parasitism are in the ratio of 1:4:8.2 (Table 4). It is not clear why the older instars are parasitized more than our experimental data would suggest. There is no evidence that the wasps are more abundant, or neap tides more prevalent, when these later instars are more common. It is conceivable that the 1st instars are for some reason relatively more difficult for the wasp to find: the arena experiments, which were continued until all the larvae had been visited, did not take into account the wasps' host-finding ability.

It would have been nice to test the importance of parental care directly by observing parasitism in maternal burrows from which the mother *Bledius* had been removed. However, the only way to remove the mother

TABLE 5. The relative "risk factor" to parasitism by *B. blediator* of each *Bledius* instar

Instar	Duration (days)	Probability of parasitism per visit	Risk factor	% Parasitized during instar (field data)
1st (in maternal burrow)	8.0	0.94	7.52	0
1st (after dispersal)	5.7	0.94	5.56	1.1
2nd	13.1	0.69	9.04	4.4
3rd	28.0	0.35	9.80	9.0

The "risk factor" is defined as the product of the duration of each instar (from WYATT, 1984, 1986) and the probability of success of parasitism on each wasp visit for that instar (data from Table 2). The first instar is divided into the maternal and post-maternal phases. It is assumed that the success of parasitism of the 1st instar beetles in the maternal burrows, were these available to the wasp, would be the same as for the 1st instars after dispersal from the maternal burrow. The data for the field levels of parasitism are also given (from Table 3).

and leave the burrow otherwise intact is to catch her when she is grazing at the surface. This is difficult to do. In any case, the results of such removal experiments would be difficult to interpret. One or two new larvae hatch each day in each burrow, and the older larvae leave the burrow at the same rate (even in orphaned burrows (WYATT, 1986)): evidently, unequivocal results about the parasitism rate in such burrows would be hard to obtain and would require a large sample size.

If protection of the larvae in the maternal burrow results from the presence of the adult female *Bledius*, what cues might the wasp use to detect the female? the most likely cue is the defensive secretion released laterally at the level of the 9th sternite (ARAUJO, 1978). The smell is quite distinctive and strong. The predator, *Dyschirius obscurus*, uses the secretion as the stimulus to attack *Bledius* and even attacks conspecifics coated with the gland contents (LARSEN, 1936). Further experiments are required to demonstrate conclusively that the mother *Bledius* deters the parasitoid and that the cues are olfactory.

The present observations suggest that adult *Barycnemis blediator* have no protection against tidal coverage: the eggs, larvae and pupae are protected inside the waterproof burrow made by *Bledius*, but the adult wasps are wetted and killed during tidal coverage (Fig. 2). This is in marked contrast to other adult saltmarsh insects, which show a variety of mechanisms for avoiding the tides: some are table to walk or fly away from the tide (*e.g.* Davis & Gray, 1966), some remain in underground burrows (*e.g. Bledius*), some have endogenous rhythms controlling their retreat to safe refuges (*e.g. Anurida*; Foster & Moreton, 1981), some (*e.g.* aphids, saldid bugs) simply cling on to the vegetation during tidal coverage (see Foster, in press). *Barycnemis blediator* is presumably able to mate and lay its eggs within one intertidal period, and there has perhaps been little selection to enable it to survive tidal coverage. It would be interesting to know if adult emergence is timed to coincide with the ebb of the tide, to allow a maximum time for copulation and egg-laying.

The occurrence of parental care in the different *Bledius* species clearly indicates that the primary function of this behaviour is protection of the young against the tides, rather than against predators and parasites. *Bledius* species characteristically live in burrows and feed on algae (Hermann, 1972). However, the only subsocial species are those from the low saltmarsh: in addition to *B. spectabilis*, these are *B. diota* Schiödte, *B. tricornis* (Herbst), and *B. furcatus* (Olivier) (Larsen, 1936). In these species, the eggs are laid around a maternal burrow, and the larvae climb into the main chamber after hatching, where they feed on algae brought down by the female. Species from the high saltmarsh and sand-dune, rarely or never covered by the tide, do not look after their young: these species include *B. fuscipes* Rye, *B. longulus* Erichson, *B. opacus* (Block) in the sand-dunes, and *B. fergussoni* Joy on sandy beaches. These species lay their eggs around a central burrow, but the egg-chambers do not lead into a main chamber and the larvae do not congregate in the main chamber after hatching. There is no evidence that the non-marine *Bledius* species look after their young. Parasitism and predation are presumably of potential importance in these species, but parental care has only evolved in those species that live low in the intertidal zone.

The ecology of animals in harsh environments is often thought to be dominated by physiological adaptations to extreme physical conditions. This attitude characterized earlier studies on intertidal organisms (see, for example, Lewis, 1964; Newell, 1970). However, it is now abundantly clear that biological factors, such as predation and competition, are also important in these extreme environments. Recent work has shown that the ecology of intertidal organisms can only be understood if both biological and physiological interactions are fully explored (*e.g.* Moore & Seed, 1985). *Bledius spectabilis* provides an elegant example of the interplay of physical and biological factors. The absolute requirement of excluding the tide has been solved by building a blockable, centralized egg-burrow, but this has created a concentration of larvae vulnerable to predation and parasitism. However, the mother defends her larvae during their most vulnerable period not only from the tides but also from the risk of parasitism.

Summary

The parasitic wasp *Barycnemis blediator* (Aubert) is an important natural enemy of the subsocial saltmarsh beetle *Bledius spectabilis* Kratz: the wasp occurs at high densities (up to 100 coccoons m^{-2}), it is very widely distributed among the beetle colonies, and life-table analysis shows that up to 15% of the immature stages can be killed by the wasp. To determine whether the mother beetle can protect her young against parasitism, we recorded in the field the reactions of individual wasps to burrows that contained either a single adult beetle, an adult and young (the larvae leave the maternal burrow about halfway through the 1st instar) or individual 1st, 2nd or 3rd instars. The wasps only went down those burrows that contained a single, post-dispersal *Bledius* larva, except once in 132 observations when a wasp was observed to go down a maternal burrow containing a female, eggs and larvae. On all other occasions, burrows containing adult *Bledius* were not entered by the wasp. None of the five hundred 1st instar larvae collected from maternal burrows in the field was parasitized. This was not because 1st instars in maternal burrows are unattractive or unsuitable for the wasp: field experiments showed that the wasps were highly successful in parasitizing 1st instar larvae taken from maternal burrows and placed in experimental burrows. Field experiments showed that the success rate of parasitism by the wasp was much higher with 1st instars (94%) than with 2nd (69%) or 3rd (35%) instars. We suggest that an important consequence of parental care in *Bledius spectabilis* is that the young are protected from attack by the parasitic wasp *Barycnemis blediator* for most of their most vulnerable phase (the 1st instar).

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Résumé

L'hyménoptère parasite *Barycnemis blediator* (Aubert) est un ennemi naturel important du staphylin subsocial des marais salants, *Bledius spectabilis* Kratz. Il est largement distribué au soin des colonies de *B. spectabilis*, avec des densités élevées (jusqu'à 100 cocons/m^2); l'analyse des tables de survie montre que jusqu'à 15% des stades immatures du staphylin peuvent être tués par l'ichneumonide.

Pour déterminer si la femelle du staphylin peut protéger sa descendance contre le parasitisme, nous avons relevé dans la nature les réactions individuelles des guêpes parasites à des terriers contenant, soit un seul staphylin adulte, soit un adulte et sa descendance (les larves quittent le terrier maternel à peu près au milieu du 1er stade larvaire), soit des larves du 1er, 2ème ou 3ème stade. Les femelles de *B. blediator* ne pénètrent que dans les terriers qui contiennent une seule larve de *Bledius* (après que celle-ci ait quitté le terrier maternel), excepté un cas sur 132 observations, où une guêpe parasite est entrée dans un terrier contenant une femelle, des oeufs et des larves; dans tous les autres cas, les terriers contenant un *Bledius* adulte n'ont pas été visités.

Aucune des 500 larves collectées sur le terrain dans les terriers maternels n'était parasitée. Ces larves ne sont pas pour autant non-attractives ou inadéquates pour *B. blediator*; des expériences faites sur le terrain ont en effet montré que l'ichneumonide parasite avec grand succès des larves du 1er stade prélevées dans un terrier maternel et placées dans un terrier expérimental.

D'autres expériences de terrain ont montré que le taux de succès du parasitisme par *B. blediator* est beaucoup plus élevé pour des larves du 1er stade (94%) que pour des larves du 2ème stade (69%) ou du 3ème (35%). Nous suggérons qu'une conséquence importante des soins parentaux chez *B. spectabilis* est la protection des larves contre l'attaque de l'hyménoptère parasite *B. blediator*, précisément au stade de développement où elles sont le plus vulnérables (le 1er stade).