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How a subsocial intertidal beetle, *Bledius spectabilis*, prevents flooding and anoxia in its burrow

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Summary. All stages of *Bledius spectabilis* Kratz (Staphylinidae) dig wine-bottle shaped burrows in the intertidal *Salicornia* zone. The adult female lays her eggs around her burrow and, by remaining with them, prevents both flooding by the tide and anoxia. Flooding is prevented by an 'ever-ready' burrow which exploits a surface tension effect and by blocking the burrow once the tide comes in. The burrow has a narrow neck (about 2 mm in diameter) leading to a living chamber 5 mm in diameter. Tides over artificial tubes in agar showed that a critical minimum neck diameter of 2–3 mm prevented sudden flooding, giving time to block the neck with mud. Blocking took about four minutes. Ensuring the burrow is reopened at each low tide is a vital role of the brooding female in anaerobic or impermeable soils. Field models of burrows became anoxic in 4 days, much less than the 4 week long egg stage. A lab model system with anaerobic agar and calculations of oxygen uptake and diffusion supported this conclusion. Mortality of orphaned larvae may be much lower, however, in burrows within large *Bledius* aggregations because of mitigating good drainage and soil aeration: larval mortality from physical causes in these burrows did not increase over 3 weeks but without the mother, 14% of the eggs were attacked by mould, and two burrows were taken over by a predatory carabid, *Dichierotrichus gustavi*, and all larvae eaten. The surface tension effects of small air-filled openings may be used by small air-breathing animals in many intertidal habitats. Like *Bledius*, other intertidal animals, including large ones, may block their burrows at high tide to keep them full of air. Maternal care, in particular the combination of behaviours which protect the brood from the tide and anoxia, enables this airbreathing insect to colonise the inhospitable habitat of the intertidal saltmarsh.

Introduction

Although the majority of insects outside the Hymenoptera show no parental care, a small but significant minority have elaborate mechanisms for looking after their young. Several hypotheses have been put forward to explain the evolution of this life-history trait. These include protection of a rich but scattered and ephemeral foodsource for the young, for example in bark and dung beetles (Wilson 1971, 1975); protection from predators or parasitoids (e.g. Evans 1977); or protection from a harsh environment.

A widely cited example of the last is an air-breathing terrestrial staphylinid beetle, *Bledius spectabilis*, which lives in the unusual and inhospitable habitat of intertidal saltmarshes (Larsen 1952 cited in eg Wilson 1971, 1975; Tallamy and Denno 1981; Eickwort 1981). Larsen suggested that the female *Bledius* plays an essential role in keeping her eggs and larvae alive in the adverse conditions of anaerobic soil and tides which cover the habitat for a depth of up to 1.7 m for up to 4 h. Circumstantial evidence suggested that the female is necessary to maintain a dry and ventilated burrow (Larsen 1952). From indirect evidence Evans et al. (1971) concluded that the tide did not reach the beetles in their burrows: if submerged directly in seawater in the laboratory the beetles went into a torpor and on return to air showed an oxygen debt. However, beetles dug up in the field when their habitat was covered by the tide showed no torpor or oxygen debt.

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In the current study I investigate if and how the female *Bledius* is able to protect her brood from flooding and anoxia. I then assess the ecological importance of this behaviour in the field.

The life cycle of the beetle is described in Wyatt (1984). In summary, the female lays her eggs in individual chambers around the wine bottle shaped maternal burrow (Fig. 1a). The female lays an egg every other day and as the egg development time is about 27 days and a mean of 24 eggs are laid per female, the female adult remains in her brood burrow for about 2 months during the summer. The newly hatched larvae move into the main chamber where they remain, feeding on algae brought down by the adult female, until about one week old when they leave to dig their own individual burrows. The young are thus guarded by the female during the egg stage and the first week of the first instar.

Bledius spectabilis at Scolt Head, the study site, were found in extensive aggregations sometimes more than 10 m^2 in area, called the *main aggregations* in this paper, as well as in small isolated aggregations, which covered only 1–2 m^2 or less, along the sides of creeks cutting into the saltmarsh. At these sites, termed *marginal zones*, the *Bledius* were often burrowing in anaerobic mud, at a level lower than the main aggregations.

Methods

Study site

Field observations and experiments were made on Missel Marsh at Scolt Head Island on the North Norfolk coast in 1979–1981 (grid ref: TF 815462). A map of the area and a description of the general saltmarsh habitat are given by Foster and Treherne (1975). *Bledius* were confined to a narrow band, between 0.8–1.5 m above Ordnance Datum (O.D.), along the banks at the level of the *Salicornietum* (*sensu* Beeftink 1977) (Wyatt 1984).

Resin casting of natural Bledius burrows

Cores, 15 cm deep and in diameter, were taken from within *Bledius* aggregations. The cores were placed in rigid plastic sleeves to prevent distortion during handling, stored at −10° C and thawed over-night before infilling with Sylgard 184 (Dow-Corning) under vacuum (see Wyatt 1984). Sylgard's low viscosity allows filling of air spaces less than 0.3 mm in diameter; it shrinks little on curing (Anon 1978); and being flexible it can be trimmed to allow measurement of the animal within the transparent resin. The complete resin infills were also used to identify the origin of soil air-space. The sorted resin casts were weighed and the volume calculated from the specific gravity of the resin.

Preparation of artificial tubes

Straight sided artificial air-filled tubes of different diameters were left in agar when vinyl tube moulds were removed. The gel (2% w/v Oxoid Purified agar (L28) in distilled water) was cast between two glass plates 200 × 200 × 2 mm, separated by a 'U' of thick walled (9.0 mm OD, 4.5 mm ID) vinyl tubing, and held together by two 3" Bulldog Clips.

The tubes were left to equilibrate with seawater overnight and drained before use. Their approximate diameters (actual diameters in brackets (see also Table 3)) were: '4 mm' (4.14), the diameter of the living chamber of a *Bledius* burrow (Fig. 1); '3 mm' (2.97); '2 mm' (2.01), the minimum diameter of the burrow neck; and '2 + 4 mm', a compound tube with a 2 mm diameter tube connected to a 4 mm diameter tube below, analogous to the compound neck and living chamber.

Tubes in anaerobic agar

As a physical model of burrows of anaerobic mud, a reducing agent, sodium thioglycolate (1.1 $g\,l^{-1}$), and a redox indicator, methylene blue (0.002 $g\,l^{-1}$), were added to the agar before casting.

Bledius behaviour in artificial tubes

One beetle was put in each tube 24 to 72 h before the start of the tide, algae were given as food, and the agar cell was placed in the tidal pressure chamber (below). The tidal chamber was sealed and all preparations made so that, when required, the tide could be started without disturbing the beetles. The lighting levels were gradually raised from near darkness to the levels needed for filming.

Laboratory simulation of tides

The pressure chamber, with a clear Perspex front and back, was adapted from one built in the Cambridge University Engineering Laboratory (Fig. 2a). The gel inside the chamber was back lit and filmed from the front. Next to the agar cell was a sensitive capillary tube manometer. The first 2 cm of the simulated tide was made by running seawater into the agar cell. This water was removed at the end of the tidal cycle with a syringe. The intervening part of the tide was produced by changing the air pressure in the chamber with compressed air (Fig. 2b). The simulated tide followed 7 tangents to a maximal field tide (Fig. 3b).

Filming the experiments

Two motor-driven Bolex 16 mm cine cameras were used. One was run at 12 frames per second for a continuous record of the first few minutes of the tide and the reaction of the beetles (if present in the experiment), and the second camera, triggered by a Synchrolapse timing unit (Pelling and Cross, London), at 1 frame every 8 s for the rest of the tide. The frame-by-frame analysis used the methods and equipment of Ellington (1984).

Effects of removing the female

The burrows from which females had been removed when grazing at the opening, together with control burrows, were dug up after one tide or after 1, 2, or 3 weeks. Wooden posts marked each burrow opening. When the neck opening had been found, a soft vinyl catheter was fed into the hole to mark it. An 8 cm diameter core, centred on the hole, was carefully broken apart to reveal the burrow.

Soil drainage

Bledius burrows were filled with seawater, using a catheter. The drainage measurements were made during a cycle of flood-

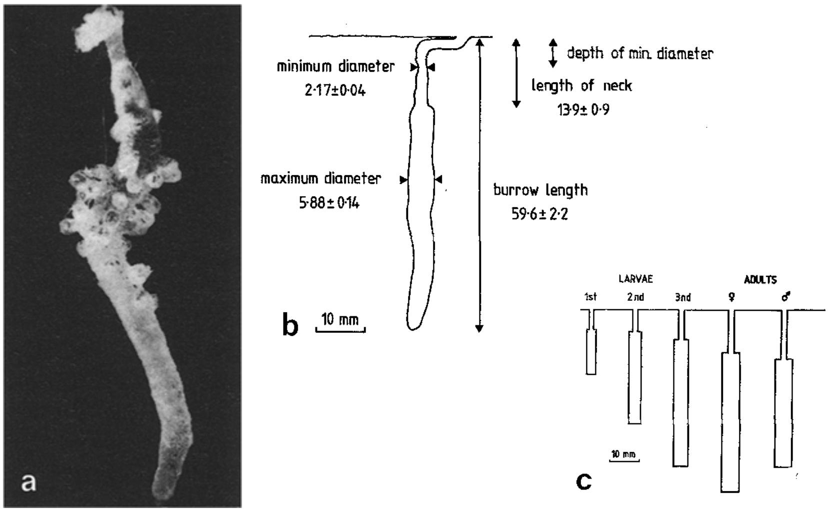

Fig. 1. **a** A *Bledius spectabilis* maternal burrow cast in Sylgard resin showing the living chamber, neck and egg chambers. The burrow is roughly circular in cross section. Photographed with dark-field illumination (Photo: G. Runnalls). **b** Diagram of the maternal burrow based on the mean values for each of the measured dimensions ($\bar{x}\pm$SE ($n=35$)). **c** Diagrams of the burrow constructed during each stage in the *Bledius spectabilis* life cycle, drawn from the mean values for each stage. The neck of each burrow is drawn as the 'minimum neck diameter' for its entire length and the living chamber as a tube of the 'maximum diameter'

ing tides, as Foster and Treherne (1976) showed that soil drainage was impaired after covering tides – the conditions when *Bledius* burrows are at risk from flooding.

Submergence of Bledius in seawater

Bledius adults or larvae, in groups of 5, were placed in 5 cm diameter gauze-bottomed plastic petri-dishes which were submerged in anaerobic seawater at 18–20° C. After 1, 4, 24, 48, 72 and 96 h submergence, twenty adults were taken from the water and allowed to recover on dry filter paper. Twenty larvae were taken after 1, 4, 12, 18, 24, 36, 48 and 60 h. The seawater had been boiled and then bubbled with nitrogen (Foster and Treherne 1976). The water was slightly warmer than the mean field soil temperature of about 16° C in July 1981.

Results

Resin fills of natural Bledius burrows

The burrows of all stages, from larvae to adults, shared a characteristic simple wine-bottle shape (Fig. 1a–c). Although there were significant regressions of all the burrow dimensions aginst the widest rigid dimension of the insect, the absolute size of some dimensions (e.g. burrow length and the length of the neck) changed rapidly with increasing size of the *Bledius*, while others changed little (e.g. minimum diameter and maximum diameter). The minimum diameter of the neck was less than 2.5 mm for all stages in the life cycle.

Burrows and the tide

Tides over air-filled artificial tubes confirmed that the shape and minimum diameter of *Bledius* burrows prevented flooding during the initial stages of the tide. Simple 4 mm and 3 mm diameter tubes filled completely within seconds of the waterfront touching the opening of the tube as the water poured over the lip of the tube (mean flood time(s): 4 mm, 8.0 ± 0.4 (8); 3 mm, 8.0 ± 1.8 (8) ($\bar{x}\pm$SE(n)). In contrast the waterfront passed over the top of the 2 mm tubes and filled only the top few millimetres of the tube to form a stable meniscus.

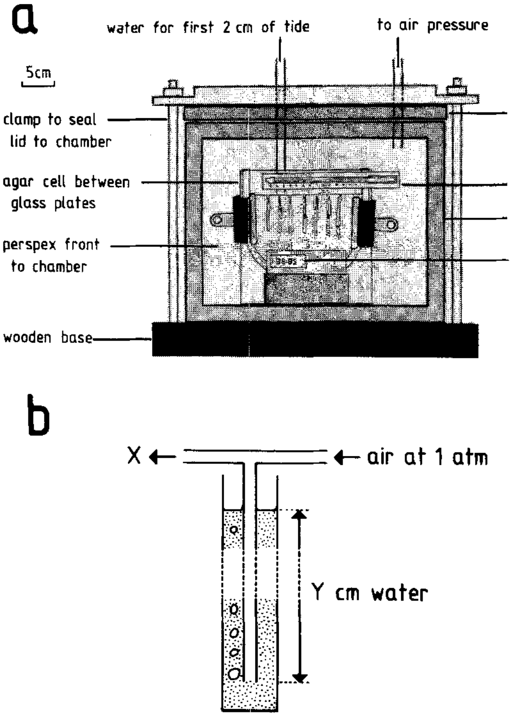

Fig. 2. **a** The pressure chamber used to simulate tides in the laboratory. **b** To produce the tidal pressure in the chamber, compressed air at 1 atm was vented through a head of water, Y, in a 2 m tall tube, giving a pressure in the chamber, to which the tube (X) leads, equal to the head of water. The increasing pressure of the rising tide was created by raising the water level slowly in the tall tube, and the ebb tide by draining water out of the tube. The water level in the tube was changed by moving the tall tube's drain (not shown) with a kymograph motor controlled by a Variac variable voltage regulator

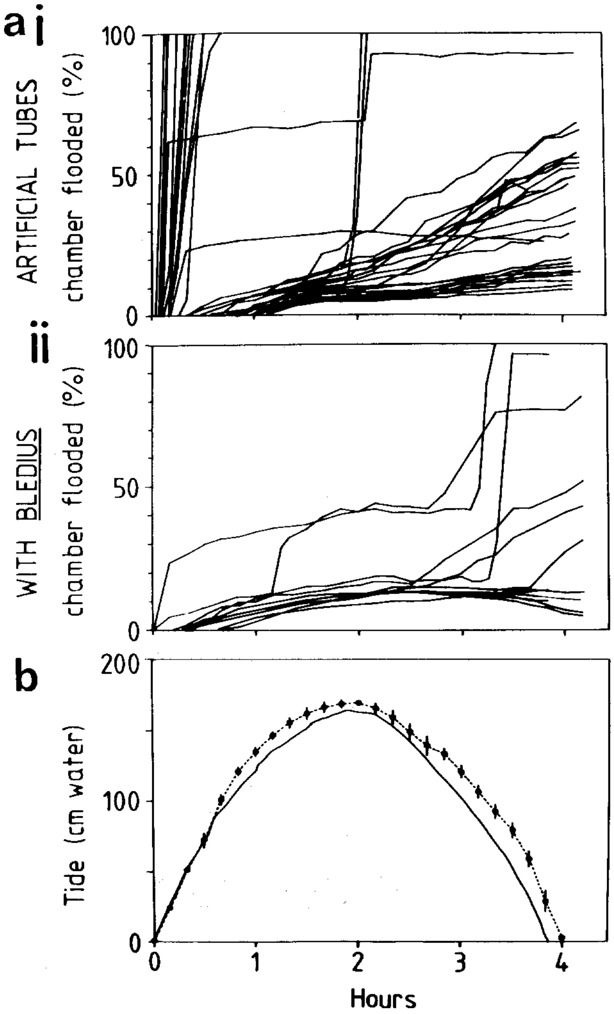

Fig. 3. **a** The percentage volume of the main chamber filled with water during a tidal cycle equivalent to the maximum field tides at Scolt Head. **i** Artificial 2+4 mm diameter tubes and tubes adapted but not occupied by *Bledius*. **ii** The same tubes occupied and modified by *Bledius*. **b** The tides simulated in the laboratory, dotted line, plotted over the depth of water covering the main *Bledius* habitat, at 1.4 m O.D., during the field tide on 27 September 1980, solid line

The critical dimension was the diameter of the opening, not the diameter of the tube below. In compound tubes, with the dimensions and shape of *Bledius* burrows, the meniscus formed in the 2 mm diameter neck prevented the 4 mm section below from flooding. The percentage volume flooded was not significantly different in 2 mm and 2+4 mm tubes (11.6±0.4% (8), 8.5±1.6% (8), $t = 1.9$, $df = 8$, $P > 0.05$). The minimum effective constriction was less than 1 cm long and, from observation of burrows made by the *Bledius* in later experiments (q.v.), 2 mm or less may be sufficient.

All the 2+4 mm tubes kept out the initial flood of seawater. Some (11/33) then gradually flooded during the first 40 min of the tide (Fig. 3ai); water slowly flowed around the air-bubble occupying the burrow and at intervals a bubble would pass up the neck and escape. Tubes which started to fill later filled in the same way. However, the majority (22/33) were less than 10% full of water after 1 h. Some of these latter tubes slowly filled with water after 2 h when the tide started to go out and the air in the tubes started to expand. The reasons for the differences between tubes are not known. Six tubes modified by *Bledius* (see following section), but not occupied at the time of the experiment, are included here because their curves were not different from the artificial tubes.

The laboratory experiments were confirmed with agar cells placed at the level of *Bledius* burrows in the field for a covering tide. All the simple 4 mm diameter tubes flooded completely within 30 s ($n = 16$). None of the compound 2+4 mm tubes flooded during the first 2 min – the limit of observation because of the turbidity of the water. At the end of the tide, many of the compound tubes were partially flooded (mean 37±6% (22) of the volume) but there was a wide range (7–100% of tube volume flooded), as in the laboratory experiments. A thick layer of silt, forming 5±0.4% (16) of the tube volume, precipitated out in the flooded 4 mm diameter tubes.

Behaviour of Bledius during tides in the lab

The beetle reacted to the tide by blocking the neck of the burrow with material taken in its mandibles from the wall of the living chamber just below the neck, treating the agar like saltmarsh mud. The block significantly reduced the probability of flooding later in the tide (Fig. 3aii) (burrows with *Bledius* compared with 2+4 mm tubes or unoccupied *Bledius* burrows in agar, $G_{adj} = 30.2$, $df = 2$, $P < 0.05$, $n = 45$). The mean delay after the start of tide before the beetles started to block (including beetles in burrows already blocked, see below) was 15.0±4.6 min (9) (range 0.25–28.5). In each case, an open neck appeared blocked in less than 1.5 min, but the beetle continued, to a total of 4.2±1.2 min (6) (range 1.0–8.8). Further material was added to the block at intervals during the tide. About 6 mm^3 of material was moved to make the block. In four burrows which happened to be blocked before the simulated tide started, the block was nonetheless added to from beneath during the tide.

The flooding of some burrows in agar (Fig. 3aii), due to failure of the block as the tide went out, is probably an artifact of the agar which does not adhere well to itself when wet.

Table 1. The dimensions (mm) of natural maternal burrows in mud (3) compared with artificial 2+4 mm diameter tubes in agar before (1) and after (2) modification by adult female *Bledius spectabilis*. Matched pairs *t*-test comparison of (1) and (2). Groups *t*-test comparison of (2) and (3). Letters mark pairs of results that are significantly different ($P < 0.05$)

Dimensions	(1) Artificial tubes 2+4 mm in diameter	(2) After modification by *Bledius*	(3) Natural burrows in field
n	≥15	≥15	≥34
Minimum diameter	2.01 ± 0.03	2.03 ± 0.16	2.17 ± 0.04
Length of burrow	57.2 ± 0.6	58.5 ± 1.6	59.6 ± 2.2
Maximum diameter	4.1 ± 0.1^{a}	4.8 ± $0.1^{a,b}$	5.9 ± 0.1^{b}
Depth of neck	18.1 ± 0.4	17.2 ± 0.9^{c}	13.9 ± 0.9^{c}
Depth of minimum diameter	–	11.6 ± 1.3	9.3 ± 0.9

When the tide had gone out the beetle reopened the burrow by dismantling the block. The beetle sometimes dug a new neck to the surface thus avoiding flooding the burrow with any water above the block.

Although the walls of the artificial tubes were considerably worked by the *Bledius*, the minimum neck diameter was not changed (Table 1). Only the maximum diameter of the burrow, where the beetles had taken material to block the neck, was significantly increased.

Moreover, the dimensions of the tubes in agar modified by the beetles were not significantly different from the natural burrows in mud in the field (Table 1), except that the maximum diameter was larger and the neck shorter in the field burrows. These differences are unlikely to be important in preventing entry of water.

Do Bledius block before the tide?
Field observations

Occasionally *Bledius* gathered algae from the mouth of the feeding gallery in the period immediately before the tide covered their burrows (11 observations). Six of these females were covered by the tide as they fed, at which point they backed quickly into the feeding gallery and down the burrow. These burrows could not have been blocked before the tide because the neck is too narrow to allow the female to turn round to block the burrow behind her when coming to the surface.

Field removal of Bledius within the main aggregations

The effect of the first tide. Just before the tide, the beetles were removed while grazing at the surface thus leaving the burrows unguarded and open. All 13 unguarded *Bledius* burrows were flooded compared with none of 20 control burrows with the *Bledius* female present. The walls of the flooded burrows were coated with a fine light-coloured sediment (similar to the sediment seen after drainage measurements and the field tests of agar tubes), soft mud filled some of the egg chambers and some eggs were knocked off their stalks. An unexpected observation was that *Bledius* burrows immediately next to the flooded burrows also showed signs of flooding.

The long-term effects. Although removing the female adult allowed the next tide to flood the burrow, after a few tides the feeding gallery was completely blocked with debris which, paradoxically, prevented flooding by later tides. The orphaned first instars did not block the burrow when the tide came in to prevent flooding. Nor did the larvae open the burrow to the surface after the tide went out. Normally the female adult maintained the burrow.

The long-term effects of removing the female adult probably depend crucially on the habitat. In the main aggregation, if mortality from predation is excluded, there was no significant difference between the number of live larvae found in the control and orphaned burrows, at weekly intervals up to three weeks (ANOVA, *df* 3, $F = 0.13$, $P = 0.94$). This suggests that initially the eggs in these orphaned burrows were hatching normally. However, after three weeks, out of a mean number of eggs per burrow of 5.0 ± 1.3 (8), 85% had been knocked off their stalks in their chambers and 14% of all eggs were covered with mould. No eggs in burrows maintained by adult females were knocked off their stalks or attacked by mould.

Two of 24 orphaned burrows were taken over by the predatory carabid beetle, *Dicheirotrichus gustavi*, which feeds on *Bledius* larvae (Wyatt 1984). No live larvae were found in these burrows; presumably they had been eaten as they hatched. *D. gustavi* were never found in maternal burrows guarded by the female *Bledius* ($n > 200$).

The low mortalities caused by the tide in orphaned burrows in *this* habitat, the main *Bledius* aggregations on Scolt Head, may be due to the good drainage within these specific sites, and to the associated good soil aeration. In the main aggregations, the burrows drained rapidly. The mean rate was 10.1 ± 3.3 cm^3 h^{-1} (13), sufficient to allow a flooded maternal burrow, with a mean volume of 1.3 cm^3, to drain in about 10 min after the tide uncovered the burrow. The drainage rate in the lowest *Bledius* site (0.8 m O.D.) was 0.7 ± 0.1 cm^3 h^{-1} (15); here a maternal burrow would empty in about 2 h. The mud in both habitats was covered by an impermeable layer, 1–2 mm thick, of fine sediment trapped in fine algae.

Within the main aggregations, macro-pore space was 3% of the total soil volume in the top 8 cm, the maximum depth of *Bledius* burrows. Of this, two-thirds was contributed by old and current *Bledius* burrows. Root-ghosts, ramifying holes left when *Salicornia* and Sea Aster (*Aster tripolium*) roots rotted away, formed the remainder. *Bledius* burrows formed about 9% of the cross-sectional area at a depth of 2 cm, giving the soil a honeycomb appearance.

Field models of abandoned Bledius burrows in anaerobic mud

The experimental removal of females, carried out in the main dense aggregations, was not feasible in the anaerobic, marginal zones because the small size of the aggregations made finding enough females grazing unlikely. Instead, *Bledius* burrow-sized holes were made in the reducing mud and blocked with a plug of mud (equivalent to the observed blocking of unguarded burrows with debris). Four days later, of 13 holes, 9 were partially or completely anaerobic; the walls of these holes had changed from the more oxidised brownish-red ferric form of iron to the reduced blue (Teal and Kanwisher 1961; Armstrong 1979). In some cases there was now a halo of reduced mud around the hole where it passed through a layer of oxidised sediment. Adjacent occupied *Bledius* maternal burrows acted as a control. All the control burrows ($n = 15$) maintained a zone of oxidised mud about 3 mm around the burrow (Fisher's Exact Test, $P < 0.01$).

Although larvae, after leaving the natal burrow, dig narrow necked burrows and also appear to show blocking behaviour, they are less successful than adults at keeping out the tide. In the anaerobic mud at the lowest part of the marginal zone, four out of the 20 larvae dug up from their burrows were dead and one was in a still flooded, anaerobic burrow (Wyatt 1984).

Table 2. The surface-area/volume ratios of 46 mm long tubes of different diameters and the length of time the oxygen would last if the tube were blocked off from the surface ('Minutes to anoxia') at a rate of oxygen uptake by the mud of 8.7×10^{-4} mm^3 mm^{-2} min^{-1}

Diameter (mm)	1	2	3	4	5	6
Surface area (mm^2)	146	295	448	603	762	924
Volume (mm^3)	36	145	325	578	903	1,301
Surface area/volume	4.1	2.0	1.4	1.0	0.8	0.7
Minutes to anoxia	60	119	175	231	286	340

Simple models of gas exchange in burrows in anaerobic mud

The estimated oxygen consumption of the mud walls of the *Bledius* living chamber was compared with the calculated rates of oxygen diffusion into the burrow. In gas-impermeable or anaerobic sediment burrows would only remain aerobic if reopened to the air by the beetle at each low tide.

The living chamber of the mean *Bledius* maternal burrow had a surface area of about 760 mm^2, giving it an oxygen consumption of 0.7 mm^3 min^{-1} from the values of Teal and Kanwisher (1961). The oxygen in a blocked airfilled burrow in impermeable mud would be used in about 4 h. If the same burrow had been flooded with seawater before being blocked, the oxygen would only last about 8 min – the percentage of oxygen in seawater at 10° C is 0.65%, compared with 21% for air. Increasing the burrow diameter prolongs the length of time the oxygen supply would last (Table 2).

If an abandoned burrow was not blocked with debris and remained open at low tide, diffusion would only maintain the living chamber's aerobic conditions if the neck and chamber were air filled (Model I, Withers 1978). If, instead, the open burrow, or neck alone, was flooded the burrow would become anoxic because of the very low diffusion constant for oxygen in water (Withers 1978). In a physical analogy using anaerobic agar, only an open air-filled tube remained aerobic. Flooded or blocked tubes became anaerobic after 1.5 and 4 h respectively.

Experimental submergence of Bledius

First instar larvae taken from maternal burrows and submerged in anaerobic seawater survived for much shorter periods than adult *Bledius*. Half the first instars died within about 16 h and all were dead before 36 h of submergence. Half of the adults died within about 50 h of submergence, 100% before 96 h. Newly hatched larvae were more vulnerable than even slightly older larvae. Only 8 of 20 larvae placed in anaerobic seawater within 10 min of hatching survived submergence for 4 h compared with 16 of 20 larvae more than 2 h old when submerged ($G_{adj}=6.64$, $df=1$, $P<0.01$).

Discussion

Bledius prevents flooding of its burrow by, first, digging burrows of a particular size and shape, and second, by reacting to the covering tide by blocking the burrow. This is the first experimental demonstration of such behaviour. At low tide the beetle unblocks the burrow. Maintaining an air-filled burrow re-opened to the air at low tide is the crucial role of maternal care in impermeable or anaerobic sediments.

Experiments on artificial tubes in agar confirmed that the characteristic narrow neck of the *Bledius* burrow prevented flooding of the larger living space below: the critical diameter was 2–3 mm. This is less than the 5 mm reported by Bretherton (1961) but agar or saltmarsh mud is very different from the glass tubes, sealed at one end, used in his experiments.

One difference between the agar system and the field may be the compression of soil air by water seeping laterally from the creeks as the tide comes in (Chapman 1960). The air is trapped under the thin impermeable surface of the saltmarsh. However, field experiments showed that this did not prevent flooding of open unguarded burrows. The flooding of modified but unoccupied tubes in agar and the unguarded burrows in the field also showed that waxes were probably not important in preventing entry of the water. The waxes on *Bledius* may waterproof the insect (cf. Staddon (1972)) but not the burrow, unlike the saltmarsh aphid *Pemphigus trehernei* which makes its cavities in the soil virtually unwettable (Foster and Treherne 1975).

The 'ever-ready' burrow of *Bledius* is proof against unexpected flooding by the tides, whose predicted heights are changed by factors such as inshore winds and barometric pressure. The burrow's narrow neck prevents a sudden flood when the tide comes in and gives the beetle ample time to construct a block across the neck, a task which it can complete in minutes. With the mud block in place the burrow is proof against the whole tide.

Unblocking the burrow at low tide is the second crucial part of parental care in *Bledius*. Unmaintained burrows become blocked with debris and, in anaerobic saltmarsh soils, burrows cut off from the air would go anoxic in hours, resulting in the loss of the whole brood. The effect was shown by field model burrows and tubes in anaerobic agar. These conclusions were supported by calculations of the rates of oxygen diffusion set against the estimated oxygen consumption of the mud walls of the burrow. A tenfold overestimation of the soil respiration rate, which is unlikely (Hargrave 1969), would not change the conclusion. The uptake of oxygen by the mud may also explain the shape of the *Bledius* burrow. In impermeable mud, only burrows with living chambers more than 4 mm in diameter would remain aerobic during the 4-h coverage by spring tides (Table 2).

However, in the dense main aggregations, where adult densities of *Bledius* approached 1,500 m^{-2}, abandoned burrows did not go anoxic when blocked. This was largely the result of the mitigating good drainage and soil aeration due in part to the effects of beetle burrows. Selection pressures nonetheless favour remaining with the brood since partial losses of brood occurred in unguarded burrows and the potential costs of remaining with the eggs are small. The first few tides flooded the unguarded burrows, and although many eggs appeared to hatch normally, some eggs were lost to mould which did not occur in brooded burrows. In addition, without the mother some burrows were taken over by the predator, *Dicheirotrichus*, with the loss of all larvae. The larvae with the mother are also protected, during their most vulnerable period, against the parasitoid wasp, *Barycnemis blediator* (Wyatt 1984). Against these losses, preventable by remaining with the brood, are set the negligible gains of leaving the brood. The gain is small since a female would have to dig a similar replacement burrow. A watertight burrow enables the adult (of either sex) to feed on algae brought down into the burrow, even at high tide when otherwise it would lose up to 8 h per day inactive while submerged.

While the majority of *Bledius spectabilis* at Scolt were in the dense main aggregations, at other sites the majority may be in anaerobic soils like the marginal zones at Scolt (eg in the Netherlands, van Wingerden et al. (1981) and Denmark, Larsen (1936, 1952)). In addition, the main aggregations occupy an ephemeral habitat, which becomes overgrown by shading plants such as *Halimione portulacoides* (Wyatt 1984) and eroded by the tide (Foster and Treherne 1978). Individuals able to rear broods in either ideal or marginal habitats will be at an advantage.

The burrows of two other saltmarsh beetles, *Heterocerus maritimus* and *H. fossor* (Heteroceridae) show a striking similarity with those of *Bledius*: a narrow neck, with a minimum diameter less than the critical value of about 2.5 mm, leads to a spherical living chamber below (Wyatt 1984). *Heterocerus* may show a similar blocking behaviour. A fourth saltmarsh beetle, *Bembidion pallidipenne* (Carabidae), digs a similar burrow (Larsen 1936). In addition, the *Heterocerus* species and *B. pallidipenne* are subsocial, guarding an egg mass in the living chamber (Larsen 1936; Clarke 1973; Wyatt 1984). Parental care in saltmarsh beetles may be dependent on the ability to make an unfloodable burrow.

Surface tension effects may be used by small intertidal air-breathing arthropods in other habitats. For example, intertidal ant nests in Mexican saltmarshes have entrances with a mean diameter of 2.6 mm (Yensen et al. 1980) and the ants reacted to the tide by partly or wholly blocking the entrance. The nests were not flooded. The air retained by small cracks and holes in rocky shores is used by air-breathing crevice fauna (e.g. Kensler 1964).

Although the possibility cannot be entirely excluded, the apparent lack of an endogenous rhythm in *Bledius* is a different approach from that taken by some of the other air-breathing invertebrates in the same habitat (see Foster and Wyatt 1985).

The surface tension effect exploited by *Bledius*, which allows an 'ever ready' but open burrow, can only be used by small animals similar in size to *Bledius* (see also Vogel 1981). Although unable to use surface tension effects, larger saltmarsh animals may share the problems caused by the slow diffusion of oxygen along water filled burrows. For example, the male fiddler crab, *Uca pugilator*, blocks its burrow as a hiding place when the tide comes in (Teal 1959). Another function of the block may be to keep the burrow full of air. This is required because, after mating with the male, the female is walled into the terminal chamber of the burrow for an incubation period of up to two weeks (Christy 1982, 1983). Teal (1959) showed that the burrows of other crab species, which flood, had terminal chambers that become anoxic (in these species the crab remained at the entrance).

Maternal care in *Bledius spectabilis*, by protecting the brood from the tide, allows it to exploit a habitat which is rich but inhospitable to terrestrial insects. The very similar behaviour of unrelated saltmarsh beetles further suggests that parental care may be an important adaptation to difficult environments.

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