

Mud-Ball Construction by *Sceliphron* Mud-Dauber Wasps (Hymenoptera: Sphecidae): A Comparative Ethological Study

Liliane Chatenoud¹, Carlo Polidori^{2,*}, Matteo Federici³, Veronica Licciardi³, and Francesco Andrietti³

¹Istituto di Ricerche Farmacologiche "Mario Negri", Milano 20156, Italy

²Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, Madrid 28006, Spain

³Dipartimento di Bioscienze, Università degli Studi di Milano, Milano 20133, Italy

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Mud-ball construction by *Sceliphron* mud-dauber wasps (Hymenoptera: Sphecidae): a comparative ethological study. *Zoological Studies* 51(7): 937-945. Mud-dauber wasps of the genus *Sceliphron* build aerial nests using mud collected at humid-soil sources and carried to the nest in the form of spherical mud-balls. We recorded and analyzed a series of video-sequences of 5 (3 native and 2 alien) species of *Sceliphron* in Italy, in order to compare their mud-ball-building behavior. Four phases were recognized: I) patrolling the ground in search of a suitable place for mud-ball building; II) removing leaves, twigs, or small stones from the chosen area; III) forming the mud-balls; and IV) flying off with the mud-balls. The duration of all these phases were similar among species, with the only exception being phase IV, which was shorter in *S. curvatum*. In all species, mud was shaped into a ball by the combined action of the legs and mandibles, but important differences also emerged in some details of this behavior. In particular, *S. curvatum* maintained the longitudinal axis of its body parallel to the ground as it worked the mud, and its antennae rapidly tapped the ball. On the contrary, in the other 4 species, the mud was pulled under the mentum and retained laterally by the 1st pair of legs, while the body axis was maintained almost vertical, and the antennae were not involved in mud shaping. Because *S. curvatum* belongs to a different subgenus compared to the other 4 species, we suggest that mud-ball-building behavior may potentially represent a useful taxonomic and perhaps phylogenetic character.
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Key words: Nesting habits, Nest material, Species-specific behaviour, Mud-dauber wasp.

Within aculeate solitary wasps (Hymenoptera: Apoidea and Vespoidea), the collection of mud as a main (mud-dauber wasps) or accessory (hole-nesting wasps) material for nest building seems to have evolved several times, as suggested by the distribution of this behaviour across different lineages (Bohart and Menke 1976, Budrys 2001).

Mud-dauber wasps of the genus *Sceliphron* Klug include solitary wasp species which build their nests using mud collected from soil in the form of spherical mud-balls (Bohart and Menke 1976). Nests are found in a variety of sheltered and dry

sites, often associated with human buildings (Bohart and Menke 1976), and are composed of a number of brood cells. Rau and Rau (1918) noted that sometimes, even when anthropogenic structures are available, wasps still build their nests on natural supports, such as vines, suggesting that places like those were the used ones before human structures were so common. Females store prey in these nests, consisting of paralyzed spiders, and then lay their eggs (Rau 1935, Polidori et al. 2007). Paralysis of the prey seems to last sufficiently long to span complete larval development, given that captured spiders were seen to remain alive for

*To whom correspondence and reprint requests should be addressed. E-mail:cpolidori@mncn.csic.es

up to 32 d (Rau and Rau 1918). Only after the construction of the 1st cell does a wasp begin to hunt for spiders to feed its larvae; then the egg is laid, and the provisioned cell is sealed before constructing another one (Grandi 1961). Following Peckham and Peckham (1905), about 40 loads are necessary for each cell, and “to build and provision one is a good day’s work”. Thus, nest building represents one of the central activities of *Sceliphron* wasps.

Major aspects of nesting and foraging biology are well documented in the literature for a variety of *Sceliphron* species (Rau and Rau 1916, Mazek-Fialla 1936, Grandi 1961, White 1962, Callan 1988, Genaro 1996, Polidori et al. 2005 2007 2009), but very little information is available on mud-collecting, mud-ball-building, and mud-carrying behaviors. Concerning the modality of mud-ball formation, the only investigation to our knowledge to date is that of Natchtigall (2001) on *S. spirifex*. Natchtigall (2001) recognized and described the following behavioral sequence of mud-collecting behavior: after a local examination of a site (1), the wasp selects a point and cleans it by removing leaf remains, little sticks, and stones, (2) forms a mud-ball with the wet soil (3) before positioning it, and flying back to the nest (4). Concerning mud-ball-carrying behavior, a recent study focused on the limiting factors which affect the mud-ball size (Polidori et al. 2009); the authors found that primarily the maximum transportable volume and secondarily the maximum transportable mass limit the size of the mud-ball carried in flight (Polidori et al. 2009). Furthermore, the position of the mud-ball during its transport (under the mentum, thus forward along the body axis) additionally reduces the theoretical maximum load due to unbalancing effects (Polidori et al. 2009; Andrietti and Polidori 2012). Lastly, concerning the fate of the mud-balls once carried to the nesting place, a detailed observation of nest structure through a geopedological analysis was recently carried out by Polidori et al. (2005). Those authors confirmed that brood cells are built by extending the mud-balls in a concentric way around the lumen, showed that the size of the particles used to build the nest does not depend on the geographical location (suggesting small-scale selection of mud), and given the low amount of organic matter in the nest material, rejected a previous hypothesis on the use of saliva by the wasps (Grandi 1961).

The aim of the present paper was to give a detailed description and when possible, to make quantitative interspecific comparisons of the

mud-collecting behavior of 5 different *Sceliphron* species: *S. spirifex* (L.), *S. caementarium* (Drury), *S. curvatum* (Smith), *S. madraspatanum* (Fabricius), and *S. destillatorium* (Illiger). These species represent almost the entire European *Sceliphron* fauna (the only species we did not sample were *S. funestum* Kohl and *S. deforme* (Smith)) (Bitsch et al. 1997, Pagliano and Negrisol 2005). Of the 5 studied species, 2 are not originally from Europe and were relatively recently introduced by humans from North America (*S. caementarium*) or southeastern Asia (*S. curvatum*) (Bitsch et al. 1997, Pagliano and Negrisol 2005, Schmid-Egger 2005, Ćetković et al. 2011). *Sceliphron curvatum* is chromatically distinctive (in particular some yellow and reddish body parts), hence easily recognized among other members of the genus found in Europe (Schmid-Egger 2005), and it belongs to the subgenus *Hensenia* (as also does the invasive *S. deforme*), while the rest of the European *Sceliphron* fauna belongs to the subgenus *Sceliphron* (Bitsch et al. 1997). Notably, nests of *S. curvatum* are composed of exposed linear series of adjacent or separated brood cells (Gepp and Bregant 1986), while in the other species, the brood cells of each nest form a more complex structure and are covered by a final thick layer of mud (Mazek-Fialla 1936, Bohart and Menke 1976, Polidori et al. 2005).

MATERIALS AND METHODS

Study area

Field data were collected at 2 sites in Italy. Data on *Sceliphron caementarium* and *S. curvatum* were collected in June 2004 near Cremona (Lombardy, Italy: 45°8'13.56"N, 10°1'44"E). Data on *S. spirifex*, *S. madraspatanum*, and *S. destillatorium* were collected in July 2008 near Alberese (Tuscany, Italy: 42°40'5"N, 11°6'23"E). At both sites, wasps were observed at local farms, where ponds were created by recent rain or irrigation, or were created by the observers (see Polidori et al. 2009); numerous nests discovered on the farms’ walls revealed that these wasp species nested copiously during the study.

Data collection

Behavioral data were obtained by analyzing videos recorded on field with a video camera Sony V600E/PAL (*plus* additional lens). The ponds,

natural or artificially created, attracted *Sceliphron* females searching for mud particularly in the late morning to early afternoon. Wasps landed at the borders of the ponds, and after briefly patrolling a restricted area, began to build mud-balls. Once a female under observation finished building the mud-ball and rose up in flight (video-recorded sequence), it was collected with an entomological net and killed by freezing, in order to confirm the species. At the Alberese site only, netted females ($n = 18$) were marked with individual combinations of colors on the thorax and/or abdomen, and then released; they were then killed at the end of the entire observation period.

At the Cremona site, a 35-min videotape was taken, and 22 sequences of mud-ball building were recorded. At the Alberese site, a 45-min videotape was recorded, including 125 sequences of mud-ball building by 18 marked wasps.

Out of these sequences, 86 (7 for *S. caementarium*, 14 for *S. curvatum*, 47 for *S. spirifex*, 5 for *S. destillatorium*, and 13 for *S. madraspatanum*) showed at least phase III and IV which were easily identifiable. In 46 of these, mud-ball building could be followed from the beginning (phase I) to the end (phase IV).

Statistical analysis

We estimated the mean, standard deviation, and minimum and maximum values of the time spent in each one of the 4 phases of mud-ball construction. In order to test for differences

between species in the time spent in each phase, we used generalized linear models (after log or square-root transformation of the data to achieve normality). An *F*-test was first performed. A non-significant *F*-test reflected a non-significant difference between the means considered; if the *F*-test was significant, a comparison between means was performed (Student's *t*-test), followed by Bonferroni's corrections for multiple comparisons. Note that it was not possible to statistically compare all of the phases using all 5 species, because certain phases were rarely recorded for some species (no comparisons were attempted for $n < 5$) (Table 1).

RESULTS

During the mud-ball-formation activity, 4 different phases were recognized: phase I, identification of the site for material collection and progressive focusing on the area; phase II, check of the collection area; phase III, mud-ball building; and phase IV, flying off.

Phase I: identification of the site for mud collection

Wasps reached the mud-collection area in flight, and then began to walk around examining the ground by tapping the soil with their antennae; the mandibles slightly sank into the ground in search of a suitable place to construct a mud-

Table 1. Average values \pm standard deviation, minimum-maximum values and sample size (n) of the time (s) spent in each phase of mud-building behavior, for each of the analyzed species. ^aOne sequence ignored during phase III (of a *Sceliphron caementarium* kicking a *S. curvatum*); ^b16 sequences ignored (phase III had already begun when the recording started); ^coutlier not included in the statistical analysis

Phase	<i>S. caementarium</i>	<i>S. curvatum</i>
Phase I	11.8 \pm 4.6, 6-17, $n = 6$	4 \pm 1.4, 3-5, $n = 2$
Phase II	12.8 \pm 7, 5-20, $n = 5$	6.8 \pm 5.3, 1-7, $n = 8$
Phase III	7.4 \pm 3, 2-11, $n = 7$	9.4 \pm 4.7, 3-19, $n = 14^a$
Phase IV	0.2 \pm 0.2, 0.08-0.5, $n = 7$	0.07 \pm 0.04, 0.04-0.16, $n = 14$

Phase	<i>S. destillatorium</i>	<i>S. madraspatanum</i>	<i>S. spirifex</i>
Phase I	6, $n = 1$	16.3 \pm 11.9, 8-30, $n = 4$	24.3 \pm 23.6, 5-120, $n = 28$
Phase II	12.5 \pm 7.8, 7-18, $n = 2$	17.7 \pm 0.6, 17-18, $n = 2$	17.3 \pm 16.1, 3-60, $n = 20$
Phase III	8 \pm 3, 4-12, $n = 5$	8 \pm 3.7, 3-15, $n = 13$	9.5 \pm 7, 2-32, $n = 47^b$
Phase IV	0.33 \pm 0.13, 0.16-0.48, $n = 5$	0.46 \pm 0.2, 0.2-0.88, $n = 13$	0.42 \pm 0.83, 0.12-5.9 ^c , $n = 47$

ball. Small flights of a few centimeters were common during this phase, at the end of which a spot of about 25 mm in diameter was identified. The duration of this phase varied widely, from 5 to 120 s (Table 1). No differences emerged between species in this phase, probably because the duration was mainly related to ground characteristics ($F = 2.07$, $d.f. = 41$, $p = 0.10$).

In general, the presence of other mud-dauber wasps did not seem to bother a wasp when it was dedicated to choosing a suitable location to begin this work. However, we identified 1 episode suggesting competition: at Cremona, a large *S. caementarium* female in phase I kicked away a smaller *S. curvatum* female in phase III (see the footnote a in Table 1).

Phase II: checking the collection area

Once an optimal location was identified, the wasp began to check the area: any leaves, twigs, or small stones were removed (Fig. 1). This phase had a duration that varied widely, from 1 to 60 s (Table 1), and it was often absent (71% of the 41 sequences recorded from phase I did not have a phase II but passed directly to phase III). No differences between species emerged in the time devoted to this phase ($F = 2.08$, $d.f. = 27$, $p = 0.11$).

Phase III: mud-ball building

When the selected area was cleaned up, mud-ball building began. The duration of this phase was much more homogeneous than that of phases I and II, varying from 2 to 32 s, with 50% of events lasting 7-10 s, for all species examined (Table 1). No statistical differences between species emerged in terms of the duration ($F = 0.21$, $d.f. = 81$, $p = 0.93$). Instead, major differences emerged in the way balls were built. *Sceliphron curvatum* showed important differences compared to the other 4 species; however, fewer less-marked differences seemed to also be present among the other species.

In *S. curvatum* (Fig. 2A, B), the mandibles first seized a piece of wet ground; then the wasp raised the material with the mandibles and the 1st pair of legs, bringing the axis of the body parallel to the ground. The wasp began working the mud, giving it a spherical shape that was rotated with the 1st pair of legs and retained with the mandibles. While the legs were pressing and spinning the spherical globule, the mandibles stripped away any excess material. During these movements, the antennae continued to rapidly tap on the ball's surface.

In *S. caementarium*, the mandibles seized

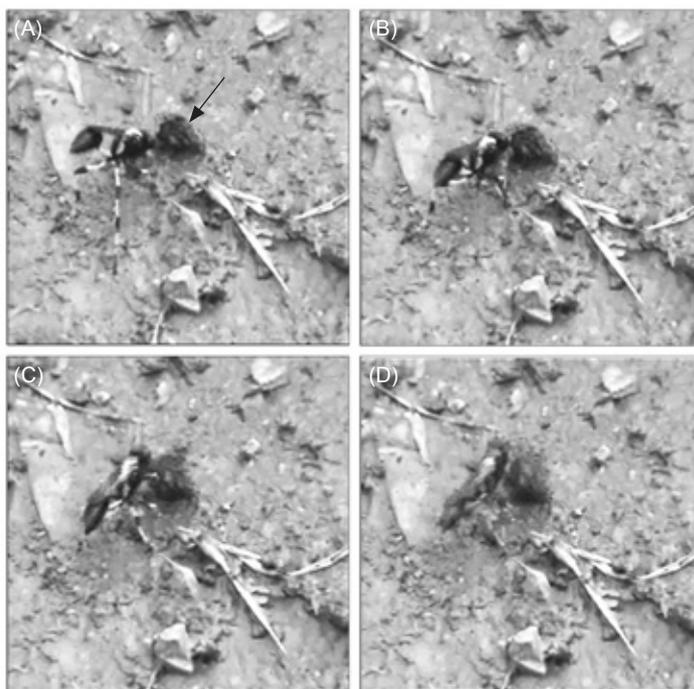


Fig. 1. A *Sceliphron spirifex* female moving a little stone (black arrow) from an area identified for mud-ball building: A-D, subsequent frames.

a piece of moist soil that was brought below the mentum and held there laterally by the 1st pair of legs. The sequence was repeated until a mud-ball was shaped by the combined action of the legs and mandibles. The abdomen followed the movement of the head leaning forward and upward and then retreated back accompanied by bending of the 3rd pair of legs. In contrast to *S. curvatum*, in the other 4 species, the antennae did not seem to play an important role in this process, as they were kept rolled and crushed to the ground when the body was brought forward, or they gently rested against the ground (Fig. 3A, B).

Sceliphron destillatorium, *S. madraspatarum*, *S. spirifex*, and *S. caementarium* acted similarly in this phase, with the body remaining in (rarely) a horizontal to (often) an almost vertical position (Fig. 4). *Sceliphron spirifex* reached more-extreme (vertical) positions of the thorax and abdomen compared to the other 3 species (Fig. 5): during this operation, the abdomen was gradually raised, and reached an extreme position (an angle of 90° between the thorax and ground, with the abdominal inclination even more pronounced) (Fig.

5). Especially in longer sequences of mud lifting (usually a consequence of dry soil forcing the wasp to spend a longer time on mud-ball building), the body followed a characteristic movement of “oscillation” around the vertical (Fig. 5: 1-4). In this phase, the mid- and hind-legs alternately assumed the role of anchor (Fig. 6A, B). At the end of this phase, the thorax and abdomen returned to a horizontal position, parallel to the ground, and the mud-ball was kept pressed with the mandibles against the thorax and, if necessary, retained laterally by the 1st pair of legs (Fig. 7A, B).

Phase IV: flying off

This was the last and shortest phase, varying from 0.04 to 0.88 s (excluding 1 outlier registered in *S. spirifex*, of 5.92 s, which was not included in the analysis). Differences in the mean phase duration were detected between species ($F = 24.9$, $d.f. = 80$, $p < 0.0001$) (Table 1). The phase IV duration in *S. curvatum* was significantly shorter than those of all other species ($p < 0.0001$). The only other significant difference after the Bonferroni

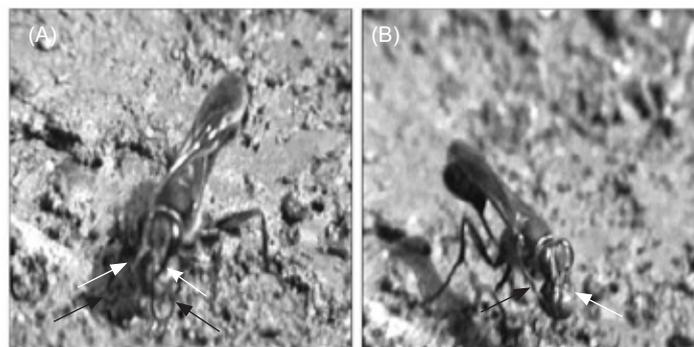


Fig. 2. Frames highlighting (A) roles of the antennae (black arrows) and mandible (white arrows) and (B) roles of the 1st pair of legs (black arrow) and mandibles (white arrow) during mud-ball building by *Sceliphron curvatum*.

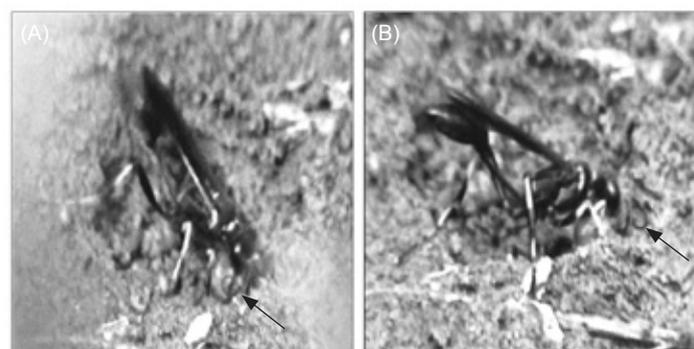


Fig. 3. Frame showing the position of the antennae (gently resting on the ground) during phase III in *Sceliphron caementarium*. (A) Almost frontal view, (B) lateral view.

correction was found between *S. madraspatanum* and *S. spirifex* ($p = 0.0008$).

The beginning of this phase was easily identified in *S. caementarium*, *S. destillatorium*, *S. madraspatanum*, and *S. spirifex* by a change in the positions of both the thorax and abdomen; these returned to a horizontal position parallel to the ground, and the mud-ball was kept off the ground,

pressed with the mandibles, and if necessary, retained laterally by the 1st pair of legs (Fig. 7). At the end of this phase, the antennae were rewound, and within a few tenths of a second, the wasp had taken flight. Conversely, in *S. curvatum*, the preparation for flying off was indistinguishable from phase III (which took place in a horizontal position).

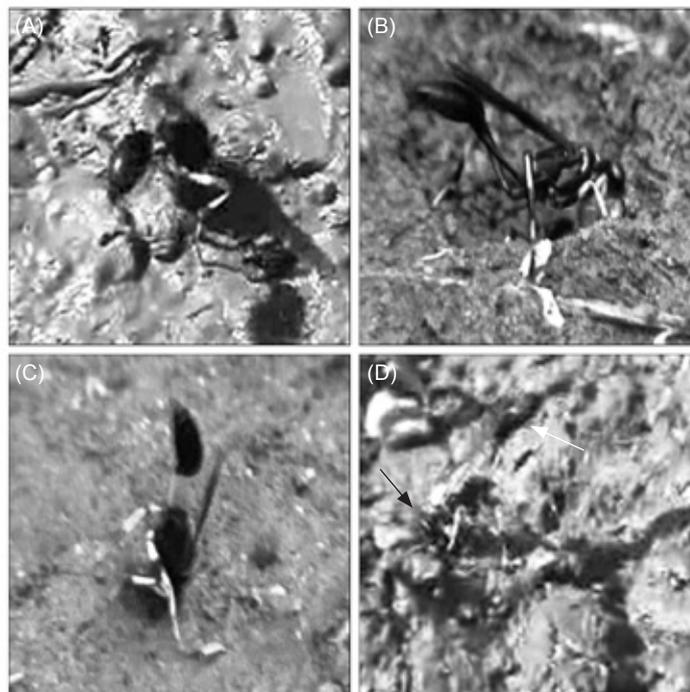


Fig. 4. Frames showing the position of the body during phase III. (A) Almost vertical position of the body of *Sceliphron destillatorium*, (B) horizontal position of the body of *S. caementarium*, (C) vertical position of the body of *S. spirifex*, (D) vertical position of the body of *S. madraspatanum* (white arrow points abdomen and black arrow points head).

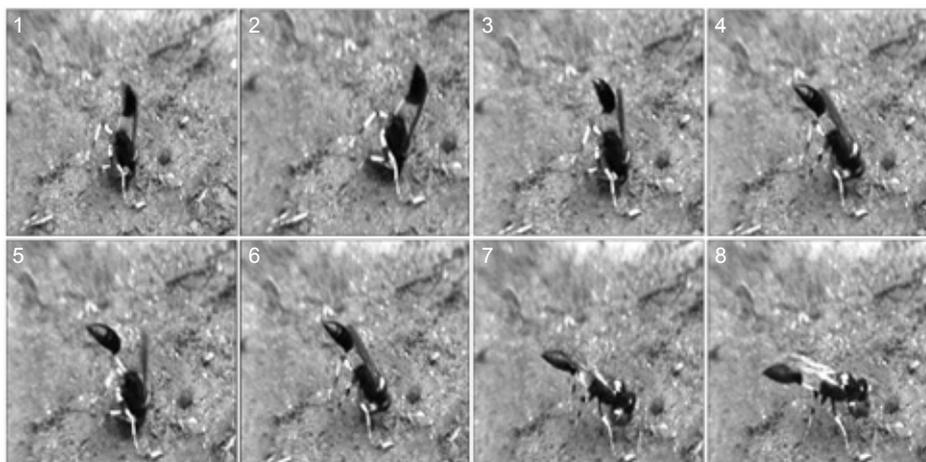


Fig. 5. Consecutive frames (1-8), highlighting different moments (in temporal order from 1 to 8) of mud-ball building in *Sceliphron spirifex* (phase III).

DISCUSSION

In general, our study confirms what was previously observed by Nachtigall (2001) who analyzed frame-by-frame the mud-building behavior of *Sceliphron spirifex*. In that study, phases II-IV together lasted from about 18-24 s, depending on the substrate (a shorter time for wet, soft soils). Such values are much higher than what was found for *S. spirifex* females studied here: considering only the 8 behavioral sequences which contained all 4 phases, the total phase II-IV time was 3.4-6.7 s (4.8 ± 1 s on average), probably because we recorded wasps on particularly soft soils.

Apart from the analysis of *S. spirifex*, which behaved similarly in our and Nachtigall's (2001) study, we here provide the 1st description of the mud-ball-building behavior of 4 other species of *Sceliphron*. A comparative analysis evidenced some similarities among species, in particular in the time spent in phases I, II, and III, but also

differences in the time required in phase IV and in the mud-ball-construction behavior (phase III).

Phases I and II were indistinguishable among species mainly due to the fact that the behavior is highly context-dependent (e.g., landmarks for site location, type of soil, and the presence of stones or sticks). Before beginning mud-ball construction (phase II), little stones were removed to prevent them from being included in the ball. This behavior limited the transport of unsuitable and/or inhomogeneous material, which could create asymmetries and breaking points in the nest walls.

The difference in the time spent in phase IV and the method of mud construction (phase III) were linked. In fact, *S. curvatum* spent the shortest time locating a mud-ball for flying off and for flying off itself, basically because it completed the previous phase (III) in a horizontal position, not in an almost vertical position as in the 4 other species. This allowed the wasps to spend less time preparing to fly away with the mud-ball.

These and other behavioral traits make *S.*

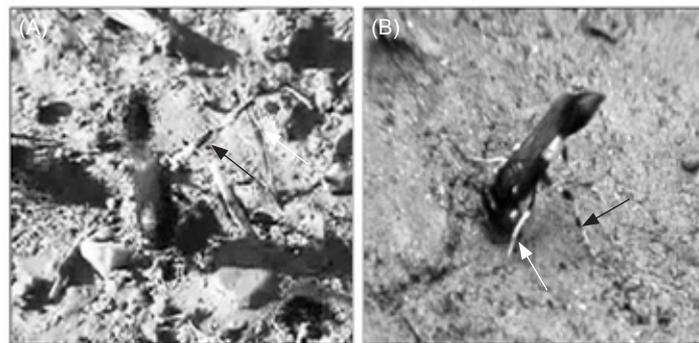


Fig. 6. Frames highlighting the role of the 3rd pair of legs (black arrows) in *Sceliphron spirifex* (phase III): (A) the wasp uses its mandibles to bring the ball of mud below the mentum, leveraging with the 3rd set of legs (here anchored to a twig (white arrow)); (B) particular role of the 2nd (white arrow) and 3rd (black arrow) pair of legs.

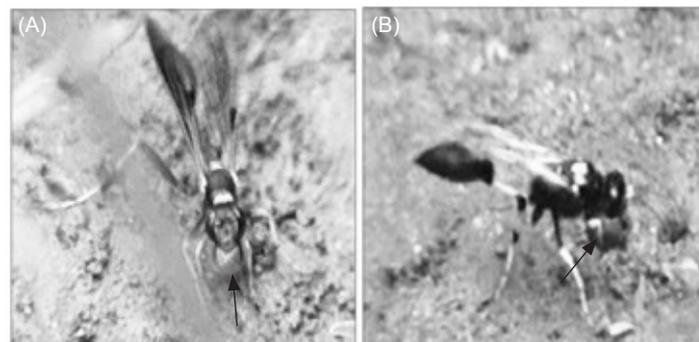


Fig. 7. Frames showing the moment just before the wasp flies off with the mud-ball (phase IV). (A) In *Sceliphron caementarium*, only the mandibles hold the mud-ball (black arrow), while the 3 pairs of legs are resting on the ground; (B) in *S. spirifex*, the mandibles hold the mud-ball which is also retained laterally by the 1st pair of legs (black arrow).

curvatum unique in the way of building the mud-ball during phase III. In particular, the use of the antennae greatly differed from the other species, since their involvement in *S. curvatum* seemed to suggest a role in mud shaping. Antennae can help better to define the globular shape of the mud-ball, but this is unlikely given that mud-balls of *S. spirifex* and *S. destillatorium*; for example, have a similarly accurate spherical shape (Polidori et al. 2009). Another hypothesis is that *S. curvatum* uses the antennae to control the humidity of the mud being shaped. Antennae of apoid wasps present specific sensilla (sensilla Ampullecea and sensilla Coeloconica, together also called “pit organs”) (Polidori et al. 2012) which are known to be CO₂, temperature, and/or humidity receptors in aculeate Hymenoptera (Yokohari 1983). These sensilla appear on the ventral and sometimes the lateroventral sides of most flagellomeres (Polidori et al. 2012), and in effect, *S. curvatum* females position the antennae with the ventral surface touching the mud-ball. Experiments are necessary to ascertain the role of the antennae in this species.

Some of the observed particular behavioral traits could be putative characters in phylogenetic reconstruction of the genus *Sceliphron*. In fact, despite behavior remaining underrepresented in phylogenetic reconstructions, possibly because the term ‘behavior’ incorporates a wide range of phenomena not all of which are equally applicable to understanding evolutionary history (discussed in Stuart et al. 2002), it is also true that comparative studies have shown that behaviour can be remarkably informative regarding the relationships of taxa (Hinde and Tinbergen 1958), in particular, if we focus on stereotyped and ritualized behaviors, such as nest building (Wenzel 1992 1993). Although we do not have robust data on *Sceliphron* phylogeny, the taxonomy of the genus is quite stable. From this point of view, *S. curvatum*, which belongs to the subgenus *Hensenia*, also had more distinct behavior compared to the other species studied here (all of which belong to the subgenus *Sceliphron*). Interestingly, such differences also remained after mud-ball construction, since the nest itself is peculiar in *S. curvatum*, with the brood cells being built and arranged on the substrate in linear rows, while in the other species, they are added one after another in layers, and then the overall structure is covered by a final thick mud layer (lacking in *S. curvatum*) (Polidori et al. 2005). We herein propose as particular putative characters for phylogenetic studies: 1) the position

of the body during phase III; 2) the involvement of the antennae in mud-ball construction (phase III); and 3) the nest architecture.

A study of mud-ball-building ethology in other species of the subgenus *Hensenia* (all its members present individual barrel-shaped nest cells which are not covered by an extra layer of mud; Hensen 1987) and an independent phylogenetic study based on morphology and/or molecular markers could provide insights into the possible use of behavior in phylogenetic studies of this mud-dauber genus.

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