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Ecology

Brood success of the mud-daubing wasp *Sceliphron jamaicense* (Hymenoptera: Sphecidae) in a desert environment

Éxito de anidación de la avispa lodera Sceliphron jamaicense *(Hymenoptera: Sphecidae) en un ambiente desértico*

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Abstract

Examination of old *Sceliphron jamaicense* (Fabr.) nests at 4 localities near the tip of the Baja California peninsula showed levels of brood success (i.e., the fraction of fully provisioned, closed cells producing viable adult offspring) between 24.6% and 58.1% per site. Failure was predominantly at the pupal stage at all localities. Successful cells are commonly reutilized by other solitary wasps, primarily *Trypoxylon (Trypargilum) dubium* Coville and *Chalybion californicum* (Sassure, 1867). There is a pronounced clumping tendency in successes and failures among nests.

Keywords: Brood success; *Sceliphron jamaicense*; Sphecidae; Araneae; Baja California Sur; Mexico

Resumen

Se llevó a cabo la revisión de nidos de *Sceliphron jamaicense* (Fabr.) en 4 localidades hacia el extremo austral de la península de Baja California. Las crías de las celdas mostraron niveles de éxito variable (i.e., la proporción de celdas cerradas y provistas con arañas que contenían adultos viables), entre 24.6% y 58.1%, según la localidad. Los fracasos se presentaron generalmente en estado de pupa. Las celdas exitosas a menudo son reutilizadas por otras avispas solitarias, sobre todo por *Trypoxylon (Trypargilum) dubium* Coville y *Chalybion californicum* (Sassure). Los éxitos y fracasos de la progenie demostraron un patrón de agregación entre los nidos.

Palabras clave: Éxito de anidación; *Sceliphron jamaicense*; Sphecidae; Araneae; Baja California Sur; México

Introduction

Sceliphron Klug, 1801 is a worldwide genus of 35 known species (Pulawski, 2016), which are relatively uniform in their morphology and habits (Bohart & Menke, 1976; Camillo, 2002). All studied species make self-standing nests of mud, each of several cells in a tight cluster (Iwata, 1976). Under sheltered conditions, the distinctive nests presumably persist virtually unchanged for years (Fye, 1965). The mother wasp stocks the cells with paralyzed spiders as brood food (Coville, 1987). The few species whose prey arrays have been studied each hunt a variety of spiders of different ecological types (Elgar & Jebb, 1998; Muma & Jeffers, 1945). In Mexico, the *lucae*

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form of *S. jamaicense* occurs in Baja California and from mid to northern Pacific Coast (Van der Vecht & Van Breugel, 1968). It is known to provision with up to 36 spider species from 14 families (Jiménez et al., 1992).

When a cell is stocked with spiders and her egg, the mother wasp seals it with mud and has no further interaction with it except often to apply a covering layer of mud up to about 3 mm thick to the nest as a whole (Bohart & Menke, 1976). Such a completed cell is not certain to yield an adult offspring. *Sceliphron. jamaicense*, like other solitary aculeate Hymenoptera, is subject to a number of nest parasites (Coward & Matthews, 1995; Crawford, 1982). These can reduce brood success —the fraction of completed cells from which adult offspring emerge— substantially. In addition, there is reason to suspect that the hard cell walls and covering layer can sometimes prevent an adult offspring from emerging, further reducing brood success. O'Neill's (2001: Table 7-3) review of brood success in 29 species of solitary wasps showed a median value of 51%, with most species between 45% and 60%. These included 4 species of *Sceliphron* with success rates of 57-64%.

An emerging *Sceliphron* offspring leaves behind an open, hard-walled cylinder of about 9 mm inner diameter and volume 1.5 ml. While no *Sceliphron* species is known to reutilize its own or conspecific cells, some other aculeates take advantage of such ready-made brood cells, a habit known as renting (Iwata, 1964; Spurway et al., 1964; Ward, 1970, 1971). Those of *S. jamaicense* in Baja California Sur are commonly reutilized by 2 other wasps: *C. californicum* and *T. (Trypargilum) dubium* (Gadar, 2009; Jiménez et al., 1992).

While it is relatively easy to find *Sceliphron* nesting sites, the search for active nests is much more laborious for humans and presumably for nest parasites. A parasite that finds 1 cell at a suitable stage for exploitation will presumably find others at the same time. This leads to the prediction of a clumped distribution of brood successes and brood failures among nests (Hunt, 1993).

Our purpose here is to assess brood success of *S. jamaicense* in a desert environment of the Cape Region of Baja California Sur, Mexico, with emphasis on variation among localities, and among nests within localities. We predicted a highly clumped distribution of successes and failures, such that if a parasite breached 1 cell it would likewise breach most of the others in the same nest.

Materials and methods

During June 2016, we collected old *S. jamaicense* nests at 4 localities in Baja California Sur: a) El Triunfo, 23°48' N, 110°06' W; b) San Bartolo, 23°45' N, 109°51' W; c) Las Cuevas, 23°32' N, 109°41' W, and d) Santiago, 23°29' N, 109°43' W. The predominant vegetation throughout the region is tropical dry forest with 645 taxa of vascular plants (5.7% are endemic). *Mimosa lagunensis*, *Erythrina flaveliformis*, *Acaciella goldmanii*, *Jatropha cinerea*, *Bursera microphilla*, and *Lysiloma microphyllum* are the most important species in this vegetation community. The climate is warm steppe, semiarid BS_0 at 500-700 m elevation and BS_1 at 700-1,550 m (León-de la Luz et al., 2012). The soils are derived from granite rocks with active erosion and surface rockiness. They are poorly developed soils of sandy loam-textured slightly acid pH but poor in organic matter (Maya-Delgado, 1988).

We collected nests on and in buildings at all localities, although at Las Cuevas most nests were from a high sandstone cave about 40 m in depth. We examined nests at the Centro de Investigaciones Biológicas del Noroeste, La Paz, dismantling them systematically and recording each cell as either successful or failed with respect to brood production. Success was evidenced either by a species-characteristic emergence hole (either 4 or 5 mm diameter, almost always through the cell closure) or reutilization by *C. californicum* or *T. (Trypargilum) dubium*, neither of which is known in any failed *Sceliphron* cell. *C. californicum* covers its nest closure with a contrasting white layer of uric acid broader than its own emergence hole (Gess & Gess, 1980, Jayakar & Spurway, 1963) (Fig. 1).

We interpreted as a failed cell one that was closed with a clear indication of offspring death inside. A mass of dead, unconsumed spiders indicate that the offspring died as an egg or larva. Death at the pupal stage was seen in a closed pupal case, often filled with the remains of a great many minute parasitoids (presumably *Melittobia* sp.; Camillo, 2002; Jiménez et al., 1992) or their pupal exuviae and a very small emergence hole through the cell wall. A very few offspring reached adulthood and then were unable to emerge from the brood cell. We disregarded the few cells made of concrete, evidently from construction sites, as well closed cells that were entirely empty, on the assumption that these latter had never been provisioned.

From successful cells we recorded reutilizations by *C. californicum* and *T. (Trypargilum) dubium*. Reutilization by *C. californicum* is evidenced by layer of white material on and sometimes around the cell top. The much smaller *T. (Trypargilum) dubium* divides the cell into 2 or (more commonly) 3 chambers, each serving as a brood cell, by means of transverse mud partitions, remnants of which persist. Occasionally a cell successfully reutilized by the former is then reutilized by the latter, although apparently never the reverse. In such a case, we recorded the cell as reutilized by *C. californicum* only. It is notable that at Las Cuevas the *C. californicum*-reutilized nests were

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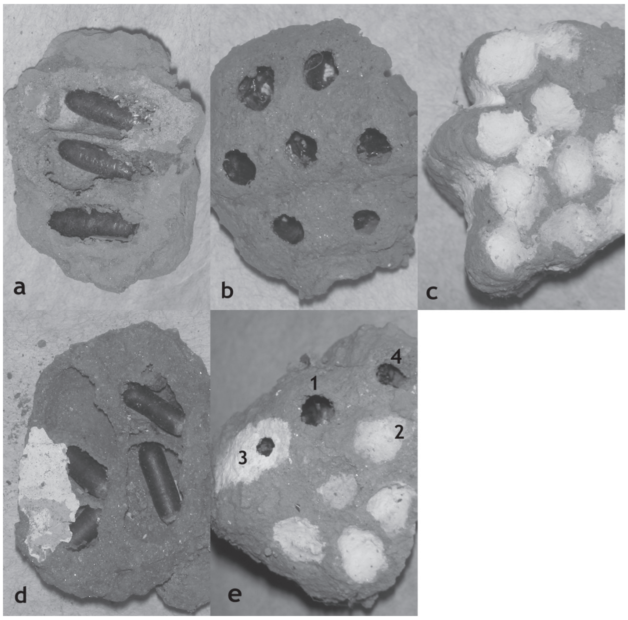

Figure 1. Outcomes of *Sceliphron jamaicense* nests after the female's nesting activity is completed. a, Nest as seen from the substrate with 3 apparently viable pupae; b, nest as seen from the outside with 7 successful emergences, prey residue visible in some cells; c, nest with successful cells reutilized by *Chalybion californicum*, with characteristic uric acid covering on and around cell closures; d, nest as seen from the substrate, with 2 successful cells each reutilized by *Trypoxylon dubium* to rear 2 offspring; e, old nest with various outcomes: successful cell with no reutilization (1), cell reutilized by *C. californicum* with presumed failure (2), cell reutilized successfully by *C. californicum* and later successfully by *T. dubium* (3), cell reutilized successfully by *T. dubium* with some later damage around the exit hole (4).

concentrated toward the inner end of the cave. Although we did not rigorously tally *T. dubium*'s brood success in reutilized cells it was plain that this was at a very low level.

At each locality we recorded the stage of failure of 100 cells chosen semi-randomly, up to 5 cells per nest.

In order to test the hypothesis of a clumped distribution of success or failure among nests, we tabulated the expected numbers of successful and failed cells among nests of 2, 3, 4 and 5 cells, given random distribution of successes.

Results

In the Cape Region of Baja California, *S. jamaicense* nests consistently in sheltered situations away from rain and direct sunlight that are not so open as to allow free passage of wind. It is our impression that this species preferentially nests in partial darkness. In the cave at Las Cuevas, we found abundant nests from near the cave mouth to all parts light enough for us to find our way with ease. This was the only locality where we found evidence of parasitism by cuckoo wasps (Chrysididae: prob. *Chrysis* sp.).

We examined a total of 2,234 cells from at least 316 old nests. Brood success varied widely among localities from 25% (El Triunfo) to 58% (Santiago) (Table 1). At all localities, brood failure was most commonly in the pupal stage (Table 2).

Trypoxylon (Trypargilum) dubium was the predominant reutilizer of *S. jamaicense* cells, with *C. californicum* also reutilizing a significant minority of cells, so that few successful *S. jamaicense* cells remained permanently vacant (Table 2).

As seen in table 3, successes and failures showed a consistent pattern of moderate clumping among nests. In each of the 4 nest sizes there were significantly more all-success and all-failure nests and fewer mixed nests than expected (X^2 test, $p = 0.02$ for 2-cell nests, $p < 0.01$ for 3-, 4- and 5-cell nests).

Discussion

We are still at a very early stage in understanding why brood success varies among species. Nelson and Starr (2016) showed that the level of success varies in a meaningful way in a renting solitary wasp. The present study may be the first to show substantial geographic variation in a species that builds its own nests.

The consistent finding that brood failure in *S. jamaicense* occurs mainly at the pupal stage at all localities appears to make good biological sense. This is the stage at which the brood reaches its greatest biomass, hence the optimal time for a parasitoid to complete its exploitation of the brood (Stehr, 1987).

Old *S. jamaicense* cells with orderly emergence holes are presumably a valuable resource for renting wasps and bees. The finding that 2 species common in the area, *T. dubium* and *C. californicum*, take advantage of them in this way confirms earlier findings.

The finding of a clear clumping tendency in success and failure among nests may be the first corroboration of the hypothesis that nest parasites locate vulnerable cells in batches, rather than randomly.

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Table 1

Brood success of *S. jamaicense* at 4 localities of Baja California Sur state, Mexico.

Locality	El Triunfo	San Bartolo	Las Cuevas	Santiago	Total
No. of nests	55	103	96	62	316
No. of cells	475	749	747	363	2,224
Successes	117	286	288	211	902
Failures	358	363	459	152	1,332
% success	24.8	44.1	38.5	58.1	

Table 2

Supplementary data from old *Sceliphron* nests at 4 localities of Baja California Sur state, Mexico. Figures of successful and failed cells are from Table 1. Below the former are numbers of cells reutilized by *Chalybion californicum* and *Trypoxylon (Trypargilum) dubium*. Below the latter are failure-stage figures estimated from samples of 100 per locality as explained in the text.

Locality	El Triunfo	San Bartolo	Las Cuevas	Santiago
Successes	117	286	288	211
Chalybion	57 (48.7%)	56 (19.6%)	129 (62.2%)	19 (9.0%)
Trypoxylon	34 (29.1%)	171 (59.8%)	48 (16.8%)	98 (46.4%)
Failures	358	363	459	152
egg/larva	13%	19%	28%	42%
pupa	86%	81%	72%	58%
adult	1%			

Table 3

Number of successful cells in nests from 2 to 5 cells. In brackets below the total number of nests is the brood-success rate for the sample, used in deriving the expected values. Further explanation in text.

	0	1	2	3	4	5	Total
Two cells							
observed	23	18	16				57
expected	17.0	28.1	11.0				(44%)
Three cells							
observed	25	7	9	12			53
expected	10.3	22.4	16.3	4.0			(42%)
Four cells							
observed	11	8	7	2	6		34
expected	4.9	12.3	11.4	4.7	0.7		(39%)
Five cells							
observed	14	5	2	3	1	7	32
expected	3.5	9.8	10.8	6.0	1.7	0.2	(36%)

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