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ON SOME FEATURES OF THE BIOLOGY OF THE RED SNAIL-NESTING BEE, *RHODANTHIDIUM STICTICUM* (FABRICIUS, 1787): PHENOLOGY, FLOWER PREFERENCE, USE OF SHELLS, FLIGHT ABILITY AND TERRITORIAL BEHAVIOUR

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ABSTRACT

The ecological and behavioural aspects of most Mediterranean bees (phenology, solitary or social behaviour, mating, territoriality, nesting and plant specialization) are still poorly known or have not been described in depth, besides a few species. That is the case of the red snail-nesting bee, *Rhodanthidium sticticum* (Hymenoptera, Megachilidae), a Mediterranean, solitary and territorial species whose biology has been described very superficially. Here, we deal with its phenology, use of snail shells other than for nesting, plant visitation and polylecty, flight ability, territoriality and mating. These results are based on our own field observations. The biology of *R. sticticum* is similar to that of other Anthidiini. It is a spring species, univoltine, active during sunny days, in the central hours. During adverse weather conditions it can be found sheltering inside snail shells, several individual sharing the same shell. Despite its polylecty, it shows preference for melittophilous plants, especially from the genus *Antirrhinum*. Males defend their territories against other conspecific males and individuals of other species, as a way of ensuring their own reproductive success.

Keywords: *Rhodanthidium sticticum*, Megachilidae, Hymenoptera, behaviour, nesting, territoriality.

RESUMEN

Algunos rasgos de la biología de la abeja roja de los caracoles, *Rhodanthidium sticticum* (Fabricius, 1787): fenología, preferencia floral, uso de conchas, capacidad de vuelo y comportamiento territorial

La ecología y el comportamiento de la mayoría de las especies de abejas mediterráneas (fenología, comportamiento solitario o social, apareamiento, nidificación, especialización en plantas) son aún poco conocidos o no han sido descritos en profundidad, salvo para contadas especies. Tal es el caso de la abeja roja de los caracoles, *Rhodanthidium sticticum* (Hymenoptera, Megachilidae), una especie mediterránea, solitaria y territorial cuya biología ha sido tratada muy superficialmente. En este trabajo se describe su fenología, el uso que hace de conchas de caracol más allá de la nidificación, la polilectia y las plantas que visita, su capacidad de vuelo, la territorialidad y el apareamiento, todo ello basado en observaciones de campo propias. La biología de *R. sticticum* es parecida a la de otros Anthidiini, pero con particularidades. Es una especie primaveral, univoltina, muy activa en días soleados durante las horas centrales. Cuando las condiciones meteorológicas son adversas se refugia en el interior de conchas de caracol, pudiendo compartirlas varios individuos (de la misma especie o incluso de otras). A pesar de ser claramente poliléctica, muestra preferencia por plantas con flores melitófilas, en especial del género *Antirrhinum*. Los machos defienden sus territorios, tanto contra otros machos conespecíficos como interespecíficamente, con un comportamiento que permite asegurar su propio éxito reproductivo.

Palabras clave: *Rhodanthidium sticticum*, Megachilidae, Hymenoptera, comportamiento, nidificación, territorialidad.

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Introduction

Bees (Hymenoptera, Apoidea) are widely known for their predominant role in pollination of wild plants and crops. Besides their importance in plants reproduction, bees also display an incredible array of behaviours concerning sociality, mating, territoriality, nesting and plant specialization (Michener, 2007). These biological aspects are partially or completely unknown for most of the species, but they are indispensable to analyze conservation status, to develop protection and conservation plans and to ensure and improve crops pollination, among other things.

The red snail shell nesting bee, *Rhodanthidium sticticum* (Fabricius, 1787) (Hymenoptera, Megachilidae), is a Mediterranean solitary bee species (Ornosa *et al*., 2008), best known for its striking red colour and its nesting behaviour, inside empty snail shells, used for sheltering, too (Romero *et al*., 2020a). The use of Gastropod shells by bees has mostly been described for nesting, but very rarely for sheltering, and it is exclusive from the family Megachilidae (Pasteels, 1977; Gess & Gess, 1999, 2008; Moreno-Rueda *et al*., 2008, Müller *et al*., 2018; Kuhlmann *et al*., 2011; Müller & Mauss, 2016). Shells offer protection against different meteorological agents, such as rain, extreme temperatures or dessication (Moreno-Rueda *et al*., 2008) and provide the perfect hiding for the larvae. Besides *R. sticticum*, three more species of *Rhodanthidium* (*R. infuscatum* (Erichson, 1835), *R. septemdentatum* (Latreille, 1809) and *R. siculum* (Spinola, 1838)) build their nests inside snail shells (Dusmet, 1908; Pasteels, 1977; Erbar & Leins, 2017). As they are obliged shell-nesters (Bosch *et al*., 1993), the presence of empty shells and the distribution of the appropriate Gastropod species influence the distribution of the *Rhodanthidium* bees themselves (Romero *et al*., 2020a), and the retraction or expansion of the snails range affects that of the snail-nesting *Rhodanthidium* species (Bogusch *et al*., 2020)

Another particular feature of *R. sticticum* is its territorial behaviour. The defence of an attractive territory to get access to females is known as "resource defence polygyny" (Emlen & Oring, 1977) and it has been widely described in Anthidiini: *Anthidiellum notatum* (Latreille, 1809) (Turell, 1976), *A. perplexum* (Smith, 1854) (Turell, 1976), *Anthidium banningense* Cockerell, 1904 (Jaycox, 1967), *A. florentinum* (Fabricius, 1775) (Batra, 1978; Wirtz *et al*., 1992; García-González & Ornosa, 1999), *Anthidium illustre* Cresson, 1879 (Alcock, 1977), *A. maculosum* Cresson, 1878 (Alcock *et al*., 1977), *A. manicatum* (Linnaeus, 1758) (Severinghaus *et al*., 1981; Wirtz *et al*., 1988, 1992; Payne *et al*., 2011), *A. palliventre* Cresson, 1878 (Villalobos & Shelly, 1991), *A. palmarum* Cockerell, 1904 (Wainwright, 1978), *A. porterae* Cockerell, 1900 (Villalobos & Shelly, 1991), *A. septemspinosum* Lepeletier, 1841 (Sugiura, 1991), *R. septemdentatum* (Nacthigall, 1997a, 1997b) and *R. siculum* (Erbar & Leins, 2017). Among these, different resources are defended and different degrees of aggressiveness are displayed. However, in *R. sticticum* this aspect has only been mentioned, but not described in detail (Torres *et al*., 2003). For males, the main point of territoriality is to keep attractive territories for females to feed on and collect nectar and pollen; thus, the objective of territoriality is mating. However, there are no descriptions of *R. sticticum* reproductive behaviour, unlike the ones on the species mentioned earlier.

Finally, from an ecological point of view, *R. sticticum* has an important role as a connector in pollination networks in Mediterranean communities (Romero *et al*., 2020b). Several authors agree in its polylecty and its importance as a generalist bee (Bosch *et al*., 1993; Müller, 1996; Aguib *et al*., 2010; Torné-Noguera *et al*., 2014; Blanco-Pastor *et al*., 2015; Vargas *et al*., 2017), but they give very little information on the plants visited. Furthermore, it is a crucial species for the survival of a number of endemic and endangered Mediterranean plants (Fernández-Mazuecos *et al*., 2013; Agulló *et al*., 2015; Blanco-Pastor *et al*., 2015; Vargas *et al*., 2017; Schurr *et al*., 2019). Polylecty is widespread among the Anthidiini (Müller, 1996; Gonzalez & Griswold, 2013), but according to Müller (1996), two *Rhodanthidium* species are oligolectic (*R. aculeatum* and *R. superbum*). Another species, *R. caturigense*, is polylectic with a strong preference for Papilionoideae (family Papilionaceae) and the rest of species, including *R. sticticum*, would be polylectic (Müller, 1996).

On the basis that the different behaviours of *R. sticticum* and diverse aspects of its biology are the same or very similar to those of related Anthidiini, especially other species of the genus *Rhodanthidium*, our aim is to shed light on those features of the biology of *R. sticticum* that were uncertain, not described or lacking in detail. Here, we present mostly descriptive results on the phenology, use of snail shells as shelters, plant visitation and polylecty, flight ability, territoriality and mating of the red snail-nesting bee.

Material and methods

Phenology and use of shells

During the spring of 2014-2018, from the beginning of March (occasionally, from February) to the end of June, field surveys were undertaken (see locations in Romero *et al*., 2020a) following nonlinear transects. During these surveys, besides the collection data, temperature, time of the day, clouds coverage and wind were recorded (the last two variables were assessed qualitatively). The surveys were undertaken at different times of the day, in the morning, during the central hours of the day and at sunset, to observe the general activity of *R. sticticum* in different moments of the day and the use of shells in particular. The presence of *R. sticticum* was assessed visually or by capturing individuals on the flight or inside snail shells, just counting the collected individuals. If the presence was visually assessed, no counting was done. Each collected shell was stored in an individual bag, to maintain the bees coming out from different shells separated.

Visited plants

Four main locations in the Iberian Peninsula were selected to assess feeding plants: Gabasa, Huesca (42.007153°, 0.416735°); Buendía, Guadalajara (40.394967°, -2.791320°); Énix, Almería (36.877929°, -2.609264°) and Nuévalos, Zaragoza (41.213594°, -1.791900°). Observation of interactions in these four locations was performed in May and June, in 2017 and 2018, during the flowering peak of most plant species. They took place during the diurnal period of flower visitor activity (from 10:00 to 17:00 h). Sampling followed nonlinear transects, covering all different species that were on bloom within the area. The surveys were done by direct observation. An interaction was considered when *R. sticticum* touched the flower reproductive parts, but not when it only landed on the flowers. To identify the plant species, samples of all the visited plants were collected. Data about plants visited by *R. sticticum* was also collected from bibliography (Bosch *et al*., 1993; Torres *et al*., 2001, 2002; Escudero *et al*., 2003; Aguib *et al*., 2010; Vargas *et al*., 2010, 2013; Carrió & Güemes, 2013; Fernández-Mazuecos *et al*., 2013; Blanco-Pastor *et al*., 2015; Schurr *et al*., 2019), in addition to personal communications (Jordi Bosch).

Flight ability, territoriality and mating

The behaviour of both, males and females of *R. sticticum*, was observed and recorded through photographs and videos during May of 2016 and 2017 in Buendía (Guadalajara), in patches of *Antirrhinum microphyllum* Rothm., to describe flight ability, territoriality, mating and general behaviour. No individuals were marked. All these traits were described by means of both direct observation and detailed observation of the recordings.

Results

Phenology

In relation to *R. sticticum* life cycle, 66 observations were accomplished in different locations, under different weather conditions, days or time of the day, between 2014 and 2019, the earliest that an individual of *Rhodanthidium sticticum* was found on February 8 in La Breña Natural Park (Cádiz) and the latest, the 17th of June in Nuévalos (Zaragoza). Most of individuals were observed or collected between mid March and the end of May (85% of the records, Fig. 1). Almost 70% of the records were obtained during sunny days. Around 75% of the observations were made during days without wind. Concerning temperatures, 71% of the records were observed under temperatures between 20 and 30 degrees Celsius. In 66% of the observations, more than five different individuals were captured.

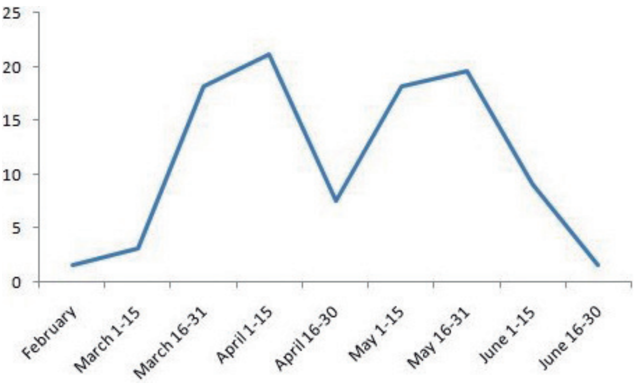

Fig 1.— Percentage of observations per fortnight, from February until July.

Fig 1.— Porcentaje de observaciones, por quincena, de febrero a julio.

Use of snail shells

Of a total of 196 collected individuals, 63% were males and 37%, females. 56% were captured flying or visiting flowers and 44% were captured inside snail shells. 86 individuals were collected in 60 shells (Fig. 2). For the individuals captured or observed on the flight, the conditions were sunny and warm, and they were recorded during the central hours of the day. Most of the captures inside snail shells took place in cold, rainy and windy days, or at late afternoon.

Fig. 2.— Male of *Rhodanthidium sticticum* emerging from a shell of *Otala lactea.*

Fig. 2.— Macho de *Rhodanthidium sticticum* emergiendo de una concha de *Otala lactea.*

Concerning the individuals found inside shells, 70% did not share it, in 13% of the shells there were two individuals, in 8% of the shells three individuals of *Rhodanthidium sticticum* were sheltering and in one shell we found six individuals (Table 1A). Two shells were shared by an individual of *Rhodanthidium sticticum* and another bee of the genus *Osmia* Panzer, 1806 and two other shells were occupied by an individual of *Rhodanthidium sticticum* and an individual of *Rhodanthidium siculum* (Table 1C). Of the 18 shells shared by two or more bees, only three were occupied by females, each of them shared by a female and a male of *Rhodanthidium sticticum*. All the other females collected in snail shells were alone in the shell (19 out of 22 individuals, 86% of all the females collected in shells) (Table 1B).

Identification of plant species visited by *Rhodanthidium sticticum*

Our field surveys showed a high diversity of plants on which *R. sticticum* feeds (Appendix 1). In particular, 43 species and 13 families of flowering plants from NE, C and SE of the Iberian Peninsula were identified. Among them, Papilionaceae (8 spp.), Lamiaceae (12 spp.) and Plantaginaceae (5 spp., all of them Antirrhineae) were the most frequently visited (Appendix 1). From literature, 38 more species belonging to 14 families were retrieved (Appendix 2). Therefore, polylecty appears to be predominant in *Rhodanthidium sticticum* diet. Despite that, *R. sticticum* shows a clear attraction for *Antirrhinum* species.

Flight ability, territoriality and mating

Males spend most of the time patrolling their territories (estimated 75% of the time), looking for females (Fig. 3) or resting on nearby rocks and branches, usually promontories where they can warm up on the sun while they watch their area. From time to time, they visit the flowers in their territory to feed on nectar, but they do this activity more rarely. *Rhodanthidium sticticum* males also perform exploratory flights when a new object enters their territory (a bag or a camera, for example), during which they remain in static flight in front of the object, observing it directly. Females

Table 1.— A. Number of *R. sticticum* individuals found sheltering inside snail shells. B. Distribution of males and females of *R. sticticum* found in shells. C. Details of localities where individuals of *R. sticticum* from Table 1B were found in shared shells. Disposition of bees inside the shells. See Romero *et al.* (2020b) for a list of all localities where individuals of *R. sticticum* were found inside shells.

Tabla 1.— A. Número de ejemplares de *Rhodanthidium sticticum* encontrados dentro de conchas de caracol. B. Distribución de machos y hembras de *R. sticticum* dentro de las conchas. C. Desglose de localidades de la Tabla 1B con *R. sticticum* encontrados compartiendo concha. Disposición de las abejas dentro de las conchas. Ver Romero *et al.* (2020b) para una lista de todas las localidades con ejemplares de *R. sticticum* en conchas de gasterópodos.

A		
N° bees in a shell	**N° shells**	**%**
1	42	70
2	8	13.33
3	5	8.33
6	1	1.67
+ other species	4	6.67

B		
Bees per shell	**N° shells**	**%**
1♂	23	38.33
1♀	19	31.67
2♀♀	0	0
2♂♂	5	8.33
1♂1♀	3	5
3♂♂	5	8.33
6♂♂	1	1.67
1♂1♂ *R. siculum*	2	3.33
1♂1 *Osmia* sp.	2	3.33

C				
Locality	**Province**	**Country**	**Shared shells**	
Castro Marím	Algarve	Portugal	2♂♂	3♂♂
			1♂1♀	1♂1 *Osmia* sp.
			1♂1♂ *R. siculum*	1♂1♂ *R. siculum*
La Herradura	Granada	Spain	2♂♂	
Espiel	Córdoba		2♂♂	2♂♂
			2♂♂	3♂♂
			1♂1 *Osmia* sp.	
Tibi	Alicante		3♂♂	
Chelva	Valencia		1♂1♀	3♂♂
Cuenca	Cuenca		6♂♂	3♂♂
			1♂1♀	

Fig. 3.— Male of *Rhodanthidium sticticum* watching a female feeding on *Antirrhinum microphyllum*.

Fig. 3.— Macho de *Rhodanthidium sticticum* vigilando a una hembra mientras esta visita una flor de *Antirrhinum microphyllum*.

spend their time looking for suitable shells for nesting, building the nest, feeding on nectar and collecting pollen for their offspring (Fig. 4).

Males protect territories with abundant flower patches, showing preference for *Antirrhinum*, Labiatae and Papilionaceae shrubs. They show a ferocious defence of the territory, chasing, attacking and striking other male intruders, but also other bees of similar or bigger size (including much bigger bumblebees or *Xylocopa violacea* (Linnaeus, 1758) individuals) and other flying insects that happen to enter their surveillance area, like flies or butterflies. We did not observe *Rhodanthidium* males attacking small flying insects in their territories.

A number of mating attempts end up in failure. Females are reluctant to the copula, so males try to catch them unaware. When a female detects the proximity of a male while feeding or collecting nectar, quickly take flight to avoid it (Fig. 5). Contact between a male and a female does not guarantee mating, either. Frequently, females wriggle out before males are able to copulate. If other male candidates are around, they usually interrupt the copula by trying to force the first male out and get the female. Even if the male has been able to start intercourse with the female, sometimes they become too heavy for the stems they are leaning on and they fall, allowing the female to escape (Fig. 6). During a successful intercourse (Fig. 7), a very characteristic sound, a continuous, rhythmic, dry clickety-clack noise can be heard, caused by the hitting of the cuticles.

Discussion

Phenology

Rhodanthidium sticticum is a very active bee during the flowering period of most Spring flowers, from March until June, but in warmer areas it is usual to find it as early as February. Most of records were taken between March and May, enlarging until mid June, matching the data from other areas of the species (Morocco, Algeria and Sicily: Kasparek & Lhomme, 2019; Algeria: Aguib *et al*., 2010). There are no records in literature or in collections about the presence of the species later than June, despite Kasparek (2019) stating, without providing any evidence ("an early spring and late autumn species with possibly two generations per year") and that it was found in Spain in October/ November. It seems to be, however, an univoltine species, like *R. siculum* or other Anthidiini bees (*Anthidium florentinum*, Fortunato *et al*., 2013). Flying period for this species starts early and is relatively long, similar to *R. septemdentatum* (Kasparek, 2019) but longer than *R. siculum* (Ortiz, 1990; Aguib *et al*. 2010; Erbar & Leins, 2017), probably due to the fact that *R. siculum* is associated to warmer climate and its optimal period is shorter (Romero *et al*., 2020a).

Sheltering in shells

Our results show that *R. sticticum* is active in sunny, not windy days, as most of the records on the flight were obtained under those conditions, corroborating a.

b.

Fig. 4.— a. Female of *Rhodanthidium sticticum* visiting flowers of *Antirrhinum microphyllum*. b. Close-up of a female of *R. sticticum* visiting flowers of *A. microphyllum*.

Fig. 4.— a. Hembra de *Rhodanthidium sticticum* visitando flores de *Antirrhinum microphyllum*. b. Primer plano de una hembra de *R. sticticum* visitando flores de *A. microphyllum*.

previous observations by other studies (Torres *et al*., 2001; Romero *et al*., 2020a). However during cloudy, rainy and windy days, or at the late afternoon, *R. sticticum* bees were mostly found sheltering inside snail shells. Apparently, *Afranthidium hamaticauda* Pasteels, 1984, *A. odonturum* (Cockerell, 1932) (Gess & Gess, 1999, 2008, 2014) and *Hoplitis conchophila* Kuhlmann, 2011 (Kuhlmann *et al*., 2011) also use snail shells for sheltering, but this behaviour has rarely been described. In those cases, the authors did not provide any information about the weather conditions or the time of the day they did their records at, but considering the location (the Namibian desert) the use for sheltering is, most likely, against the heat of the central hours of the day or to sleep at night. Despite the existence of detailed descriptions of the nesting

Fig. 5.— Female of *Rhodanthidium sticticum* facing a male who was trying to copulate.

Fig. 5.— Hembra de *Rhodanthidium sticticum* enfrentándose a un macho que intenta copular con ella.

behaviour of *Rhodanthidium* bees inside snail shells (Pasteels, 1977; Erbar & Leins, 2017), sheltering has never been described before on this species.

Of all the bees found in shells, 30% were sharing and most of them were males. This behaviour is in contrast with the territoriality usually showed when they are flying and there are no previous records of other bees in their adult phase sharing shells. The reasons could be diverse. Individuals sharing the same shells they were born from (phylopatry), high density of individuals and few shells disposable, which would force them to share, or the urge to rapidly find a shelter when the weather suddenly changes. The fact that most of the sharing bees were males is probably due to the higher proportion of males. The male-female proportion (3 males per female) is unlike other Anthidiini bees (*Anthidium florentinum*, Fortunato *et al*., 2013).

Plant visitation and polylecty

Our results indicate low specificity of *R. sticticum* for particular plant species, in concordance with previous studies (Bosch *et al*., 1993; Aguib *et al*., 2010; Torné-Noguera *et al*., 2014). Specificity of bees to special feeding plants has been described as a rare phenomenon (Cane & Sipes, 2006; González-Varo *et al*., 2016). Indeed, *R. sticticum* appears to be a polylectic bee (Bosch *et al*., 1993; Müller, 1996), although it probably has a preference for bee-specialized (melittophilous) plants, such as *Antirrhinum, Linaria* and Papillionaceae (Blanco-Pastor *et al*., 2015; Vargas *et al*., 2017), and for deep-corolla flowers, like the Labiatae (Appendices 1–2). The flowers of melittophilous plants show fusion of petals (sympetaly) and a bipartite perianth that hinders the entrance of insects other than bees and other Hymenoptera (Vargas *et al*., 2010; Blanco-Pastor *et al*., 2015). This flower structure protects the floral reward, thus ensuring that individuals reaching the bottom of the flower will most certainly get it, a reason why it could be so appreciated by *R. sticticum* females. It is particularly noteworthy the interest showed by *R. sticticum* in *Antirrhinum* species all through its range (see Appendices 1–2), proving that it is not a local preference, but a general one.

Flight ability

Flight ability by *R. sticticum* is identical to that described for *R. septemdentatum* (Nachtigall, 1997a). It is fast and precise and could be hypothesized that its good sight is, in part, responsible for it. Very few and recent studies concerning sight and perception have been performed on solitary bees (Loukola *et al*., 2020), but multiple discoveries in bumblebees confirmed learning skills, precise colour and shape discrimination (Giurfa *et al*., 1995; Spaethe *et al*., 2001; Dyer & Chittka, 2004; Solvi *et al*., 2020). The exploratory behaviour observed in *R. sticticum* males (and probably females, though it was not detected) is very similar to that described by Loukola *et al*. (2020) in *Osmia* bees when searching for suitable nesting sites.

Territoriality and mating

Rhodanthidium sticticum males, like most Anthidiini bees, are usually larger than females (García-González & Ornosa, 1999; Michener, 2007; Erbar & Leins, 2017), a probable consequence of territoriality, which helps them to get and defend better territories (Severinghaus *et al*., 1981; Villalobos & Shelly, 1991). Defence of territory is widely spread among Anthidiini (Michener, 2007). Selection of territories where deep-corolla flowers are predominant has been previously reported for *Anthidium maculosum* (Alcock *et al*., 1977), *A. septemspinosum* (Sugiura, 1991), *Anthidiellum notatum* and *A. perplexum* (Turell, 1976). Deeper corollas difficult females from seeing nearby males and escaping them. In the closely related species *R. siculum*, however, the defended territory is not rich in feeding flowers, but in empty shells for nesting (Erbar & Leins, 2017). In this case, *R. siculum* males take advantage of females when they are inside the shells. Despite the abundance of deep-corolla flowers, many attempts at copulation were unsuccessful, due to the lack of receptiveness and the ready flight of the females, just like in other Anthidiini bees (Wainwright, 1978; García-González & Ornosa, 1999; Erbar & Leins, 2017).

In the case of *R. sticticum*, the fierce defence is oriented not only against other males, but also against

a. b.

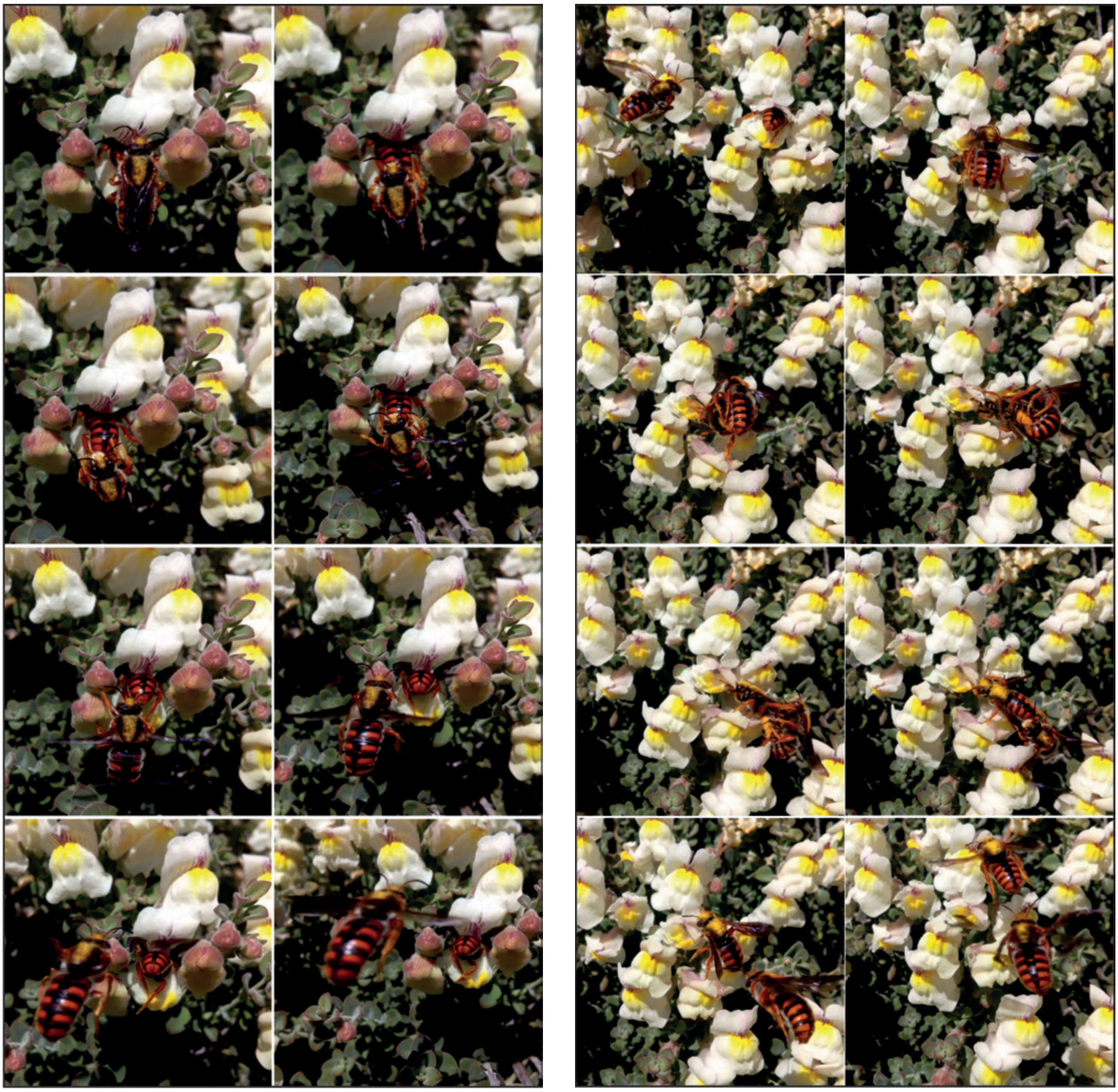

Fig. 6.— a. Male of *Rhodanthidium sticticum* unsuccessfully trying to mate while a female was visiting flowers of *Antirrhinum microphyllum*. b. Male of *R. sticticum* harassing a female and unsuccessfully trying to copulate with it while it fed on flowers of *A. microphyllum*.

Fig. 6.— a. Macho de *Rhodanthidium sticticum* intentando, sin éxito, copular con una hembra mientras esta visita flores de *Antirrhinum microphyllum*. b. Macho de *R. sticticum* acosando a una hembra e intentando, sin éxito, copular con ella mientras se alimenta en flores de *A. microphyllum*.

individuals from other species. This behaviour has also been described for *A. florentinum*, against much bigger *Xylocopa violacea* bees (García-González & Ornosa, 1999), for *A. maculosum* against hawkmoths (Alcock *et al*., 1977) or for *A. palmarum* against *Anthophora* bees (Wainwright, 1978). A different behaviour is showed by *Anthidiellum notatum* and *A. perplexum*, smaller Anthidiini that do not strike the intruders, but just chase them until they leave the territory (Turell, 1976). On the other extreme are *Anthidium manicatum*, whose males bear long spines at the end of the abdomen which they use to hurt or even kill intruders (Wirtz *et al*., 1988), and *R. septemdentatum* (Nachtigall, 1997b), that attacks the wings of the intruders. That extremely aggressive behaviour was not observed in *R. sticticum*, but it could not be discarded. Interspecific territoriality as shown by *R. sticticum* and the other species has been

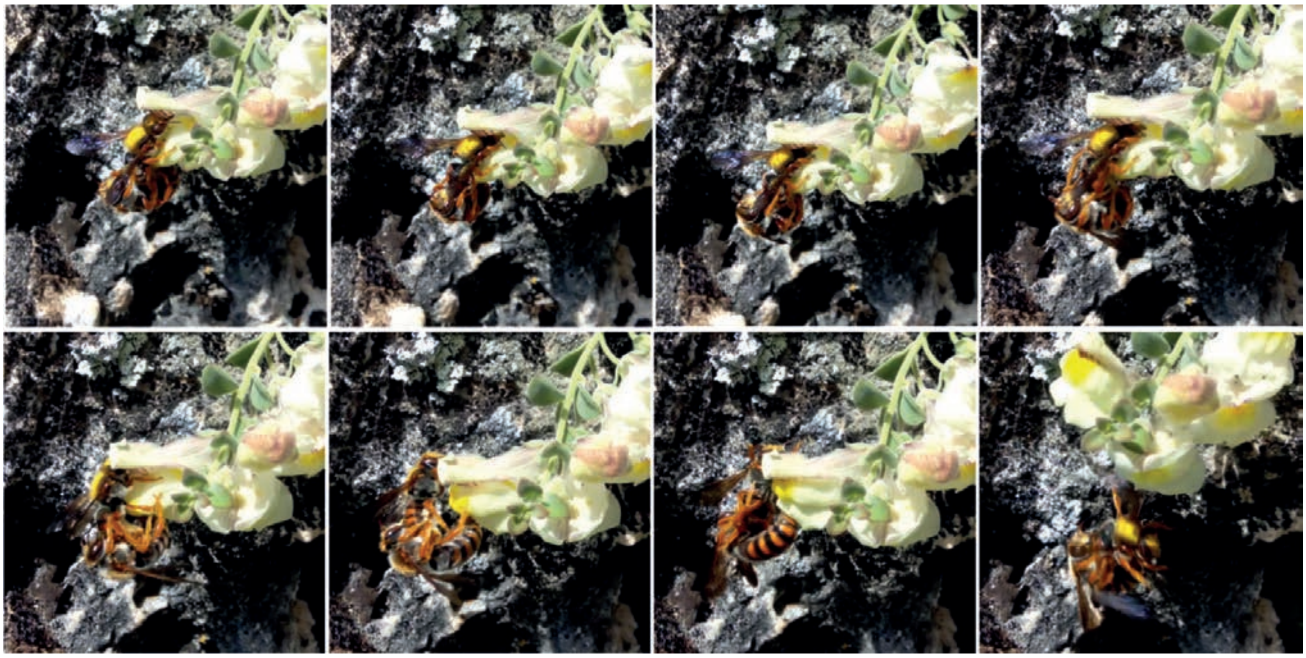

Fig. 7.— *Rhodanthidium sticticum* copulating.

Fig. 7.— *Rhodanthidium sticticum copulando.*

described as a way of keeping competitors of females (for nectar and pollen) away and maintaining the attractiveness of the territory (Severinghaus *et al.*, 1981; Wirtz *et al*., 1988).

The fact that some males enter the alleged territories of other males may indicate several things: territories overlap, new or young males looking for a territory, or opportunistic wandering males, without a territory. The presence of wandering males was described in *A. florentinum* (García-González & Ornosa, 1999), *A. maculosum* (Alcock *et al*., 1977), *A. manicatum* (Severinghaus *et al*., 1981), *A. septemspinosum* (Sugiura, 1991) and *R. siculum* (Erbar & Leins, 2017), fighting because of territories overlapping was described for *A. banningense* (Jaycox, 1967) and territories changing ownership was described for *A. manicatum* (Severinghaus *et al*., 1981). The three causes seem to be plausible for *R. sticticum*, but further observations including individuals measuring and marking should be done to confirm it.

Unlike most bees, Anthidiini females are polyandrous, whereas males exhibit resource defence polygyny (Michener, 2007). In this context, it has been demonstrated that, in *A. manicatum*, the last copulating males have an above-average chance of fertilizing the female's egg (Lampert *et al*., 2014), and the same has been theorized for *A. florentinum* (García-González & Ornosa, 1999). The polyandrous behaviour of *R. sticticum* females, together with the polygyny by males, could be driven, as it happens in *A. manicatum* and most certainly in *A. florentinum*, by spermatic competence.

Conclusions

Phenology, polylecty, flight ability, territoriality and mating behaviour in *R. sticticum* are similar to those of other Anthidiini, but with some particularities. *Rhodanthidium sticticum* is a spring bee, whose period of activity depends on the latitude and the availability of flowers. It is on the flight during sunny, warm and non-windy days. On the contrary, it takes shelter inside snail shells in cold, rainy, windy days, late afternoon and at night. When hiding inside the shells, it usually shares the shells with other individuals of the same or other bee species. It is a polylectic bee, but with preferences for certain plant groups (Anthirrineae, Labiatae, Papillionaceae), particularly attracted to *Antirrhinum* flowers. Territories defended by males are, usually, flower patches from the mentioned groups, both because they provide an attractive amount of nectar and pollen for the females and because this deep-corolla flowers prevent females from escaping the copula. Males attack other *R. sticticum* males entering their territory, as well as individuals from other flying insects, in an attempt to maintain the attractiveness of their territories and to prevent other males from mating, presenting a behaviour probably driven by spermatic competence.

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Appendix 1.— Plant species visited by *Rhodanthidium sticticum* in Buendía Dam, Guadalajara (B); Cabo de Gata, Almería (C); Énix, Almería (E); Gabasa, Huesca (G); Monzón, Huesca (M); Nuévalos, Zaragoza (N).

Apéndice 1.— Especies de plantas visitadas por *Rhodanthidium sticticum* en la presa de Buendía, Guadalajara (B); Cabo de Gata, Almería (C); Énix, Almería (E); Gabasa, Huesca (G); Monzón, Huesca (M); Nuévalos, Zaragoza (N).

Species	Family	Loc.	Species	Family	Loc.	Species	Family	Loc.
Thapsia villosa L.	Apiaceae	E	*Marrubium supinum* L.	Lamiaceae	E	*Hedysarum boveanum* Bunge ex Basiner	Papilionaceae	G
Anthemis arvensis L.	Asteraceae	G	*Phlomis lychnitis* L.	Lamiaceae	B, E, N	*Lathyrus clymenum* L.	Papilionaceae	E
Carduus nigrescens Vill.	Asteraceae	N	*Rosmarinus officinalis* Spenn.	Lamiaceae	B, N	*Medicago sativa* L.	Papilionaceae	N
Cirsium arvense (L.) Scop.	Asteraceae	B	*Salvia verbenaca* L.	Lamiaceae	B, N	*Ononis natrix* L.	Papilionaceae	E
Helichrysum stoechas (L.) Moench	Asteraceae	B	*Sideritis tragoriganum* Lag.	Lamiaceae	B	*Anthirrinum pulverulentum* Lázaro Ibiza	Plantaginaceae	N
Anchusa undulata L.	Boraginaceae	B	*Thymus hyemalis* Lange	Lamiaceae	E	*Antirrhinum microphyllum* Rothm.	Plantaginaceae	B
Echium plantagineum L.	Boraginaceae	N	*Thymus mastichina* (L.) L.	Lamiaceae	N	*Antirrhinum molle* L.	Plantaginaceae	G
Echium sabulicola Pomel	Boraginaceae	E	*Thymus vulgaris* L.	Lamiaceae	B, M, N	*Antirrhinum mollissimum* (Pau) Rothm.	Plantaginaceae	E
Echium vulgare L.	Boraginaceae	B, E	*Thymus zygis* Loefl. ex L.	Lamiaceae	M	*Antirrhinum* sp.	Plantaginaceae	Taza, Morocco
Cistus albidus L.	Cistaceae	E	*Lavatera maritima* Gouan	Malvaceae	C	*Antirrhinum* sp.	Plantaginaceae	Tazzekka, Morocco
Convolvulus althaeoides L.	Convolvulaceae	E	*Anthyllis cytisoides* L.	Papilionaceae	E	*Linaria aeruginea* (Gouan) Cav.	Plantaginaceae	N
Gladiolus communis L.	Iridaceae	E	*Anthyllis terniflora* (Lag.) Pau	Papilionaceae	E	*Reseda lutea* L.	Resedaceae	B
Gynandriris sisyrinchium Ker Gawl.	Iridaceae	E	*Bituminaria bituminosa* (L.) C.H.Stirt.	Papilionaceae	B, E	*Reseda phyteuma* L.	Resedaceae	E
Ballota hirsuta Benth.	Lamiaceae	C	*Coronilla juncea* L.	Papilionaceae	E	*Ruta angustifolia* Pers.	Rutaceae	B
Lavandula multifida L.	Lamiaceae	E	*Coronilla minima* L.	Papilionaceae	B	*Asphodelus fistulosus* L.	Xanthorrhoeaceae	E

Appendix 2.— Plant species visited by *Rhodanthidium sticticum* obtained from bibliography.

Apéndice 2.— Especies de plantas visitadas por *Rhodanthidium sticticum* obtenidas de la bibliografía.

Species	Family	Location	Source
Hedysarum coronarium L.	Papilionaceae	Constantine, Oum El Bouaghi (Algeria)	Aguib *et al.*, 2010
Cytisus linifolius (L.) Lam.	Papilionaceae		
Carduus sp.	Asteraceae		
Centaurea nicaeensis All.	Asteraceae		
Crepis vesicaria L.	Asteraceae		
Malva sylvestris L.	Malvaceae		
Helianthemum caput-felis Boiss.	Cistaceae	Punta de la Glea (Alicante)	Agulló *et al.*, 2015
Linaria almijarensis Campo & Amo	Plantaginaceae	Cabra (Jaén)	Blanco-Pastor *et al.*, 2015
Linaria amoi Campo ex Amo	Plantaginaceae	Canillas de Aceituno (Málaga)	
Linaria anticaria Boiss. & Reut.	Plantaginaceae	El Torcal, Antequera (Málaga)	
Linaria depauperata subsp. *hegelmaieri* (Lange) De la Torre, Alcaraz & M.B. Crespo	Plantaginaceae	Arenal de Petrel (Alicante)	
Linaria platycalyx Boiss.	Plantaginaceae	Zahara de la Sierra (Cádiz)	
Linaria polygalifolia Hoffmanns. & Link	Plantaginaceae	Monte Gordo (Algarve, Portugal)	
Cistus sp	Cistaceae	Cazorla or Les Garrigues (not specified)	Bosch *et al.*, 1993
Hippocrepis sp	Plantaginaceae		
Quercus sp	Fagaceae		
Centaurea linifolia L.	Asteraceae	El Garraf Natural Park (Barcelona)	Bosch, pers.com.
Anagallis arvensis L.	Primulaceae		
Biscutella laevigata L.	Brassicaceae		
Centaurea paniculata L.	Asteraceae		
Cistus albidus L.	Cistaceae		
Cistus salviifolius L.	Cistaceae		
Convolvulus althaeoides L.	Convolvulaceae		
Dorycnium hirsutum (L.) Ser.	Papilionaceae		
Gladiolus communis L.	Iridaceae		
Iris lutescens Lam.	Iridaceae		
Muscari neglectum Guss. ex Ten.	Asparagaceae		
Orobanche latisquama (F.W. Schultz) Batt.	Orobanchaceae		
Phlomis lychnitis L.	Lamiaceae		
Ranunculus gramineus L.	Ranunculaceae		
Rhaponthicum coniferum (L.) Greuter	Asteraceae		
Rosmarinus officinalis L.	Lamiaceae		
Sideritis hirsuta L.	Lamiaceae		
Thymus vulgaris L.	Lamiaceae		
Fumana hispidula Loscos & J. Pardo	Cistaceae	Dehesa del Saler (Valencia)	Carrió & Güemes, 2013
Antirrhinum microphyllum Roth.	Plantaginaceae	Entrepeñas (Guadalajara)	Escudero *et al.*, 2003
Linaria viscosa (L.) Chaz.	Plantaginaceae	SE Iberian Peninsula	Fernández-Mazuecos *et al.*, 2013
Linaria clementei Haens.	Plantaginaceae	Málaga	
Linaria salzmannii Boiss.	Plantaginaceae	Málaga	
Astragalus tragacantha l.	Papilionaceae	Calanques National Park (Marseille, France)	Schurr *et al.*, 2019
Antirrhinum microphyllum Rothm.	Plantaginaceae	Bolarque (Guadalajara)	Torres *et al.*, 2001, 2002
Antirrhinum charidemi Lange	Plantaginaceae	Cabo de Gata (Almería)	Vargas *et al.*, 2010
Antirrhinum australe Rothm.	Plantaginaceae	Benaocaz and Zahara de la Sierra (Cádiz)	Vargas *et al.*, 2017
Antirrhinum barrelieri Boreau	Plantaginaceae	Mojácar-Carboneras (Almería)	
Antirrhinum hispanicum Chav.	Plantaginaceae	Guéjar Sierra; Trevenque; Abrucena (Granada)	
Antirrhinum microphyllum Rothm.	Plantaginaceae	Buendía dam, Sacedón (Cuenca)	
Antirrhinum molle L.	Plantaginaceae	Gabasa (Huesca)	
Antirrhinum mollissimum (Pau) Rothm.	Plantaginaceae	Énix (Almería)	
Antirrhinum pulverulentum Lázaro Ibiza	Plantaginaceae	Nuévalos (Zaragoza)	