ISSN 0013-8738, Entomological Review, 2014, Vol. 94, No. 3, pp. 330–336. © Pleiades Publishing, Inc., 2014.
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Nesting Ecology of the Wasp *Sceliphron destillatorium* (Illiger, 1807) (Hymenoptera, Sphecidae) in the Crimea

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Received November 10, 2013

Abstract—The nests of *Sceliphron destillatorium* in the Crimea were mainly built in attic spaces of houses and in various uninhabited buildings, and consisted of 3–39 (on average 16.5) cells. Twelve species of spiders from 11 genera of 4 families with predomination of Araneidae and Oxyopidae were recorded as prey. One nest cell contained 4–13 (on average 7.9) spiders, mostly adult ones. Successful development of *S. destillatorium* progeny was recorded in 48.6% of the cells; 26.5% of the progeny died from parasites: *Amobia pelopei* (16.0%), *Chrysis taczanovskyi* (4.3%), and *Melittobia acasta* (6.2%); 24.9% of the progeny died for unknown causes at the egg (13.0%) or prepupal (11.9%) stage. Nests of 17 other wasp and bee species from the families Pompilidae (2 species), Vespidae (4), Colletidae (1), and Megachilidae (10 species) were found in abandoned nest cells of *S. destillatorium*. The abundance of *S. destillatorium* has noticeably decreased in the last ten years, possibly due to immigration of a congener, *S. curvatum*, which has more diverse trophic links and a significantly higher rate of nesting success.

DOI: 10.1134/S001387381403004X

The genus *Sceliphron* Klug, 1801 counts 35 species in the world fauna (Pulawski, 2013). Practically all the more or less studied species show a tendency for synanthropization and range expansion under the direct or indirect action of man (Harris, 1992; Kazenas, 2001; Mader, 2013). Five species of this genus inhabit Ukraine and the Crimea: *Sceliphron spirifex* (Linnaeus, 1758), *S. caementarium* (Drury, 1773), *S. madraspatanum tubifex* (Latreille, 1809), *S. destillatorium* (Illiger, 1807), and *S. curvatum* (F. Smith, 1870) (Shorenko, 2005; Shorenko and Konovalov, 2010; Protsenko et al., 2012; Fateryga and Kovblyuk, 2013). Of them, *S. m. tubifex* and *S. spirifex* are rare in the Crimea. They were found there comparatively recently, in 1987 (Shorenko, 2003) and 1996 (Shorenko, 2005), respectively; yet, considering their rarity, they may have occurred earlier in the Crimea. *Sceliphron curvatum* was first found in the Crimea in 2000 (Shorenko, 2003), but already by 2003 it started to be recorded as a mass species in some parts of the peninsula, mainly on its south coast (Fateryga, 2007; Fateryga and Kovblyuk, 2013). One more species, *S. caementarium*, was found in the Crimea in 2007 (Shorenko, 2007; reported as *Sphex caementarium*). Thus, only *S. destillatorium* has evidently inhabited the peninsula for a very long time. The collection of Vernadsky Taurida National University (Simferopol) includes specimens of this species collected in the Crimea at the end of the XIX century (Protsenko et al., 2012), but most probably, *S. destillatorium* was common there much earlier.

The nesting biology of wasps of the genus *Sceliphron* is studied rather well. All the species mould separate cells out of mud and store spiders as provender for their brood. Wasps of the nominotypical subgenus *Sceliphron*, represented in the Crimea by *S. spirifex*, *S. caementarium*, *S. m. tubifex*, and *S. destillatorium*, build adjoining cells with common side walls and, as a rule, cover them with a common layer of mud (Jayakar and Spurway, 1967; Minoransky et al., 1970; Ferguson and Hunt, 1989; Weaving, 1995; Mader, 2013). Representatives of the subgenus *Hensenia* Pagliano et Scaramozzino, 1990, which includes *S. curvatum*, build nests consisting of separate, isolated or only partly adjoining cells, usually without a common cover (Iwata, 1976; Harris, 1992; Schmidt-Egger, 2005).

Of considerable interest are data on the influence of adventive species of the genus *Sceliphron* on the aboriginal wasp fauna, in particular on the biologically close congeners. Since *S. destillatorium* has been present for a very long time in the Crimea, as well as in other regions of Europe, it may be regarded as a member of the aboriginal fauna. Wasps of this species belong to the already formed natural and anthropogenic ecosystems with established trophic associations. New invading species may disrupt these associations by fitting into the same food chains that are used by the aboriginal species *S. destillatorium*. It was shown, for instance, that the abundance of *S. destillatorium* noticeably decreased after the appearance of the adventive species *S. curvatum* in some regions of Austria in 1979 (Gepp, 2003).

To assess the possible influence of adventive species upon the abundance of *S. destillatorium* in the Crimea, we studied the specific traits of its nesting ecology in this territory. Data on the nest structure of this species have been published earlier and they are not considered in detail in this communication. The goal of our research was to describe the nesting places selected by the females of *S. destillatorium*, the provender composition, the nest parasites, reproductive success, and also the species composition of other wasps and bees which use the cells of *S. destillatorium* for building their nests.

MATERIALS AND METHODS

Research was carried out in 2002–2011; part of the data was obtained in 1996 and 2000. The nests were collected in the following localities of the Crimea: the city of Yalta and its environs; Orlovka and the Cape Aya state wildlife reserve within the Sevastopol city council territory; Gvardeiskoe, Simferopol District; Karadag Nature Reserve of the National Academy of Sciences of Ukraine and the Lisya Bay regional landscape park within the Feodosiya city council territory; Kipchak gully, Tarkhankut Peninsula, Chernomorsk District; the Opuk Nature Reserve, Kerch Peninsula, Lenino District. Altogether, over 100 nests of *S. destillatorium* were collected. The exact number of the collected and examined nests could not be determined because in some cases they occurred as aggregations of closely adjoining nests built by several females. Some of these aggregations, found in Kipchak gully under the roof of a rural toilet building, were up to 1 m in diameter and up to 50 cm high. In such cases, only the lowest, recently built nests were selected for examination.

Nests were mainly collected during the winter season, after which the cells were opened in the laboratory and their composition was studied. The number of cells was determined for 21 nests which could be successfully separated from the substrate and the adjoining nests. The nest cell composition, reproductive success, the nest parasites, and the tenants settling in abandoned cells were studied in 534 cells. The number of stored spiders was determined in 44 cells; 104 spiders found in 12 cells were identified to species.

Indirect assessment of the dynamics of the species abundance was based on the surveys of nests in the attics of seven houses in Yalta, carried out every 2–5 years from 1996 to 2011. To avoid repeated counts, the counted nests were either removed or marked with special labels.

RESULTS

The Nest Structure, the Nesting Substrate, and the Dynamics of Abundance

Nests of *S. destillatorium* consist of one or two rows of cells situated one above the other and made of silt or clay. Female wasps collect building material on the banks of reservoirs, puddles or near other water sources. Nests may be also built of sea sand mixed with silt; such nests were found only in Kipchak gully. After building the first two or three cells the female covers them with a common layer of building material. Then it either starts building a new nest or continues to add new cells to the same nest, consecutively covering each cell with a common layer of mud. Fully completed nests look like clots of mud attached to the substrate and contain from 3 to 39 cells (on average 16.5 ± 4.8; $n = 21$).

Since the nests of *S. destillatorium* need protection from rain, they are usually built in shelters. The great majority of nests of this species were found in the attic space of multistoried buildings, on walls, under eaves, and inside one-storey nonresidential premises, under bridges and inside other engineering structures. Only four nests were found outside buildings, three of them placed under rocks and one, in the hole left behind by the decomposed tree root on the slope of an earth road. All these nests were found in the Cape Martyan and Cape Aiya nature reserves, on the south coast of the Crimea. It should be noted that these protected territories have a special "Eumediterranean" type of landscape which is not to be found on the rest of the peninsula (Bagrova et al., 2003). The natural conditions of this landscape may be similar to those which existed in the territory of the species range before it extended to the north due to synanthropization.

Table 1. The dynamics of the number of nests of *Sceliphron destillatorium* (Illiger) in different years, based on surveys in the attics of seven houses in Yalta

Number of nests	1996	2000	2002	2006	2011
New	14	6	1	1	0
Old	37	8	8	7	2

Thus, the main nesting places of *S. destillatorium* in the Crimea are house attics in urbanized areas and small separate buildings in the natural and weakly transformed landscapes. In the latter case, due to the rarity of reliable rain shelters, the nests often occur in aggregates. In house attics, providing numerous shelters suitable for nesting, the wasps always build separate nests.

The data obtained by the surveys of *S. destillatorium* nests in house attics in Yalta testify to gradual reduction of the abundance of this species (Table 1). Nests were numerous at the end of the XX century, whereas starting with 2000, their number within the constant survey area gradually decreased, and the latest surveys carried out in 2011 did not reveal any new nests at all. These data are supported by the results of observations in nature. We did not conduct special surveys of the relative abundance of *S. destillatorium* adults; however, based on the collection data from the south coast of the Crimea, in the recent years this species occurred several times less frequently than at the end of the XX century.

The Composition of Provender

The prey of *S. destillatorium* found in the nest cells consisted of 12 species of spiders from 11 genera and 4 families (Table 2). The families Araneidae, Oxyopidae, and to a lesser degree Thomisidae prevailed in the number of specimens. The family Tetragnathidae was represented by only one specimen. The greatest part of the prey consisted of mature spiders all of which were females; only 16 specimens out of 104 were juveniles. All the spiders found in the cells were rather large, about 1 cm long. Judging by the species composition of the prey, it may be assumed that females of *S. destillatorium* hunt spiders in tall grass (~50 cm), in the upper part of the herbaceous layer. Among the victims there were representatives of both web-building and vagrant groups of spiders. Thus, *S. destillatorium* is trophically associated with spiders about 1 cm long living in the upper part of the grass stand, and does not show selectivity as to the taxonomic composition and age groups of its prey. One cell contained from 4 to 13 spiders (on average 7.9 ± 0.6; $n = 44$).

The Nest Parasites and Progeny Survival Rates

Among 534 studied nest cells of *S. destillatorium*, there were 20 empty cells which did not contain eggs or provender but had been sealed by the female. Of the remaining 514 cells, adults had emerged only from 250; the progeny in 136 cells perished due to infestation by parasitoids and inquilines; in 128 cells it perished from an unknown cause (Table 3). The greatest part of *S. destillatorium* progeny (16%) perished as the result of infestation by the inquilinous flies *Amobia pelopei* (Rondani, 1859) (family Sarcophagidae) which infest wasp cells at the provisioning stage by laying several eggs in each cell. The fly larvae feed on the spiders stored in the cell; having demolished the food reserve, they can bore through the cell walls and penetrate into the adjoining cells to continue feeding. Puparia of *A. pelopei* were found in *S. destillatorium* nests in practically all the localities where our material was collected. Another entomophage feeding on the wasp progeny, the cuckoo wasp *Chrysis taczanovskyi* Radoszkowsky, 1876 (family Chrysididae), occurred much rarer; it was recorded in Yalta, in Kipchak gully, and in Gvardeiskoe. The fraction of the progeny which perished from *Ch. taczanovskyi* was little more than 4% (Table 3). The cuckoo wasps also infest nest cells of *S. destillatorium* at the provisioning stage but lay only one egg per cell. The biology of *Ch. taczanovskyi* has not been known before; according to our data, this species also infested nests of *Euodynerus disconotatus* (Lichtenstein, 1884) (Hymenoptera, Vespidae) built in abandoned cells of *S. destillatorium* (see below).

The mortality of *S. destillatorium* progeny due to the parasitoids *Melittobia acasta* (Walker, 1839) (Hymenoptera, Eulophidae) was a little over 6% (Table 3). These parasitoids penetrate into the host nest cells already after they have been sealed, and infest prepupae or pupae at the initial stages of their development. Larvae of *M. acasta* were found in the nests of *S. destillatorium* in two localities: in Kipchak gully and in Lisya Bay. Of the progeny which perished from other factors (with no apparent cause), an approximately equal number of individuals perished at the egg stage and at the prepupal and pupal stages (Table 3). Thus, not more than a half of *S. destillatorium* progeny survives under the impact of parasites and other factors in the Crimea.

Table 2. The taxonomic composition of spiders found in the nest cells of *Sceliphron destillatorium* (Illiger)

Family, species	Number of specimens
ARANEIDAE	
Aculepeira armida (Savigny et Audouin, 1826)	11 ♀
Araniella cucurbitina (Clerck, 1758)	8 ♀
Argiope lobata (Pallas, 1772)	2 juv.
Cyclosa sierrae Simon, 1870	1 ♀
Mangora acalypha (Walckenaer, 1802)	3 ♀, 1 juv.
Neoscona adianta (Walckenaer, 1802)	9 ♀, 2 juv.
OXYOPIDAE	
Oxyopes heterophthalmus (Latreille, 1804)	31 ♀, 1 juv.
Oxyopes lineatus Latreille, 1806	2 ♀
TETRAGNATHIDAE	
Tetragnatha montana Simon, 1874	1 ♀
THOMISIDAE	
Misumena vatia (Clerck, 1758)	4 ♀
Runcinia grammica (C. L. Koch, 1837)	1 ♀, 2 juv.
Thomisus onustus Walckenaer, 1805	17 ♀, 8 juv.

Table 3. Mortality of progeny of *Sceliphron destillatorium* (Illiger) due to parasites and other factors

Species of parasite or other mortality factor	Number of cells	Fraction,%
Melittobia acasta (Walker, 1839)	32	6.2
Chrysis (*Cornuchrysis*) *taczanovskyi* Radoszkowsky, 1876	22	4.3
Amobia pelopei (Rondani, 1859)	82	16.0
Death of egg or larva at early stages of feeding	67	13.0
Death of prepupa or pupa in cocoon	61	11.9
Total number of dead individuals	264	51.4

Nesting of Other Wasp and Bee Species in Nests of S. destillatorium

Nests of *S. destillatorium* are never reused by wasps of this species, so that after the emergence of the progeny the vacant cells remain open, looking as ellipsoid-cylindrical cavities with a weakly expressed neck at the distal end. They vary in size from 6.5 × 22 to 12 × 36 mm. Such cavities make convenient nesting places for some other wasp and bee species. Of the 250 examined cells in which development of *S. destillatorium* had been successfully completed, more than 200 were occupied by nests of tenants. In total, 215 nests of wasps and bees of 17 species from 8 genera and 4 families were found in the empty cells of *S. destillatorium* (Table 4).

As a rule, tenants use the cells of *S. destillatorium* from which adults have successfully emerged. In some cases the bees *Hylaeus* sp. (family Colletidae) settled in cells from which the flies *Amobia pelopei* had emerged; in other cases, the bees *Osmia caerulescens* (Linnaeus, 1758) (family Megachilidae) settled in cells from which the cuckoo wasps *Chrysis taczanovskyi* had emerged. These two tenants are small and can use the openings left by the emerging parasites, which have a smaller diameter than those left by emerging adults of *S. destillatorium*. However, most tenant species can only nest in cells from which wasps have emerged.

The most common tenants of *S. destillatorium* nests are megachilid-bees, especially *Hoplitis manicata* Morice, 1901, and various species of the genus *Osmia* Panzer, 1806. The second place is occupied by wasps of the family Vespidae, among which most of the nests belonged to *Ancistrocerus auctus* (Fabricius, 1793).

Table 4. The taxonomic composition of tenant wasps and bees nesting in abandoned nest cells of *Sceliphron destillatorium* (Illiger)

Family, species	Number of nests
POMPILIDAE	
Agenioideus cinctellus (Spinola, 1808)	1
Auplopus carbonarius (Scopoli, 1763)	1
VESPIDAE	
Euodynerus (*Euodynerus*) *dantici* (Rossi, 1790)	1
Eu. (*Euodynerus*) *disconotatus* (Lichtenstein, 1884)	14
Ancistrocerus auctus (Fabricius, 1793)	28
A. gazella (Panzer, 1798)	4
COLLETIDAE	
Hylaeus sp.	3
MEGACHILIDAE	
Hoplitis (*Hoplitis*) *manicata* Morice, 1901	57
Megachile (*Chalicodoma*) *lefebvrei* Lepeletier, 1841	1
M. (*Eutricharaea*) *apicalis* Spinola, 1808	9
M. (*Pseudomegachile*) *ericetorum* Lepeletier, 1841	2
Osmia (*Helicosmia*) *caerulescens* (Linnaeus, 1758)	11
O. (*Helicosmia*) *dimidiata* (Morawitz, 1870)	8
O. (*Helicosmia*) *melanogaster* Spinola, 1808	6
O. (*Helicosmia*) *niveata* (Fabricius, 1804)	33
O. (*Osmia*) *bicornis* (Linnaeus, 1758)	31
O. (*Osmia*) *cornuta* (Latreille, 1805)	5

Wasps of the family Pompillidae and bees of the family Colletidae only sporadically colonized nests of *S. destillatorium* (Table 4).

In the Karadag Nature Reserve, the bees *Anthophora* (*Anthophora*) *plumipes* (Pallas, 1772) (family Apidae) settled in old nests of *S. destillatorium* but did not use the vacated cells for nesting; instead, they gnawed out their own cells and nest channels in the substrate without any reference to the original wasp cells. The same arrangement of cells (across the original wasp cells) was found in 6 nests of *Hoplitis manicata* which were located in old *S. destillatorium* nests built mostly of sea sand in Kipchak gully.

Nests of many tenant species of wasps and bees were found in cells of *S. destillatorium* after they had been used by other species of tenants. Especially often the nests were placed in cells earlier inhabited by the bees *H. manicata*. Nests of *Euodynerus disconotatus*, *Osmia niveata* (Fabricius, 1804), and other species were found in the abandoned nests of this bee. Nests of *Osmia caerulescens* (Linnaeus, 1758) and *Megachile apicalis* Spinola, 1808 were often located in abandoned nests of *Osmia bicornis* (Linnaeus, 1758); nests of *M. apicalis* were also found in abandoned nests of *Ancistrocerus gazella* (Panzer, 1798).

Thus, *S. destillatorium* is an important component of ecosystems since the nests of these wasps form the core of a peculiar complex which includes not only parasites of this wasp but also a great number of tenant species using the cells of *S. destillatorium* as nesting places, and members of the consortium associated with them.

DISCUSSION

The main nesting localities of *S. destillatorium* in the Crimea are attics of houses and various non-residential buildings. This trait distinguishes this species from another congener common in the Crimea, *S. curvatum*, whose nesting biology was described in our previous communication (Fateryga and Kovblyuk, 2013). Nests of *S. curvatum* are usually built in human dwellings. Thus, *S. destillatorium* and *S. curvatum* do not compete for suitable nesting places. However, as shown by observations, the abundance of *S. destillatorium* decreased considerably after the appearance of *S. curvatum* in the Crimea.

The object of competition between *S. destillatorium* and *S. curvatum* may be trophic resources, i.e., the objects of hunting. The prey of *S. destillatorium* in our material included 12 species of spiders from four families. Six other species of spiders from the same families except Oxyopidae were found in the prey of *S. destillatorium* in Dzhankoy District of the Crimea by Onchurov (2000). According to his data, mature spiders, mainly from the family Araneidae, prevailed among prey. The known prey of *S. curvatum* is more diverse: it includes spiders from nine families with prevalence of Araneidae, Salticidae, and Philodromidae (of the families whose representatives are hunted by *S. destillatorium*, only Tetragnathidae were not found). In addition, judging by the species composition of the spiders found in cells of *S. curvatum*, this wasp hunts not only in tall grass but also in the crowns of shrubs and low trees. Unlike that of *S. destillatorium*, the prey of *S. curvatum* mostly includes juvenile spiders (Fateryga and Kovblyuk, 2013).

Only one spider species, *Oxyopes lineatus* Latreille, 1806, was found in the prey of both wasp species. Since wasps of the genus *Sceliphron* are not strictly specialized predators, the absence of common species in their provender may be explained by the fact that the material came from different localities. Nests of *S. curvatum* were mainly studied by us in the environs of Yalta and in the Karadag Nature Reserve, whereas nests of *S. destillatorium* were studied in Orlovka and in Kipchak gully, and only three cells of this species containing spiders were collected in Yalta. Thus, it is possible that if these two species nested together, their prey ranges would partially overlap in such a way that the prey range of *S. destillatorium* would be almost completely included into that of *S. curvatum*. In this case, the latter species would win trophic competition, since it has a more diverse prey composition and also hunts juvenile spiders, thus reducing the future abundance of mature spiders which are consumed by *S. destillatorium*.

Two more factors may lead to a decrease in abundance of *S. destillatorium* due to competition with the adventive species *S. curvatum*. The first factor is the presence of only one generation a year in *S. destillatorium*, whereas *S. curvatum* may develop in two generations a year (Fateryga and Kovblyuk, 2013). The second factor is low reproductive success of *S. destillatorium*: successful development of progeny was recorded only in 48.6% of its cells. Among species of the genus *Sceliphron* a lower reproductive success (28.2–33.8%) was recorded only in *S. spirifex* in South Africa; this was explained by the fact that its nests, unlike those of *S. destillatorium*, have no common cover and consequently are less protected from enemies (Weaving, 1995). The reproductive success of other species studied was 56.2–72.1% (Hunt, 1993; Weaving, 1995), whereas the survival rate of progeny of *S. curvatum* in Ukraine was 64.4% (Fateryga and Kovblyuk, 2013).

Thus, a decrease in abundance of *S. destillatorium* in the Crimea is most probably related to competition with *S. curvatum* which appeared in 2000. Competition between these two species is intensified due to the faster reproduction of *S. curvatum* owing to its bivoltinism and a higher reproductive success. Under the present conditions, the abundance of *S. destillatorium* in the Crimea can be stable only in comparatively well-preserved steppe landscapes, for instance, on the Tarkhankut and Kerch Peninsulas where *S. curvatum* has not yet been recorded. However, on Kerch Peninsula one more adventive species, *S. caementarium*, was recorded (Shorenko, 2007) whose influence on the abundance of *S. destillatorium* has not been studied yet.

Since nests of *S. destillatorium* constitute an important resource needed for nesting of some tenant species (other wasps and bees whose nests were found in the abandoned cells), a decrease in abundance of *S. destillatorium* in the Crimea due to competition with adventive species will affect a number of species of solitary bees and wasps. For instance, the use of nest cells of *S. destillatorium* as the main nesting substrate by the wasp *Ancistrocerus auctus* must have been established in the nest building instincts of the latter species (Ivanov and Fateryga, 2003; Fateryga, 2007). If the nests of *S. destillatorium* become scarce, *A. auctus* can be expected to become less abundant or to switch to nesting in other substrates. Thus, population decline of *S. destillatorium* is an important ecological phenomenon, which may not be of practical importance yet, but is certainly of theoretical significance.

ACKNOWLEDGMENTS

The authors are grateful to Yu.G. Verves (Institute of Plant Protection, National Academy of Sciences of

Ukraine) for identification of flies, A.N. Kilimnik (Odessa State Ecological University, Odessa, Ukraine) and K.V. Martynova (Donetsk National University, Ukraine) for identification of cuckoo wasps, and also to S.K. Gess (Albany Museum, Grahamstown, South Africa) and Yu.V. Protsenko (Taras Shevchenko National University of Kyiv, Ukraine) for the literature provided.

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