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Behavioural and ecological data on *Dryudella stigma* (Panzer, 1809) (Hymenoptera, Astatidae) with the first description of the mature larva

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Abstract

Data on the bionomics of *Dryudella stigma* (Panzer, 1809) in Poland are presented. The larva is described for the first time for a European *Dryudella*, and second in the world with only larva of *D. immigrans* described before. The egg stage lasts 2–3 days, and the larval stage 11–14 days. The praepupal stage lasts the longest time and overwinters in a cocoon from mid-July to the end of May. The female provisions with an average of seven bug nymphs per cell, mainly of *Aelia acuminata* (Linnaeus, 1758) (Pentatomidae), less often *Ceraleptus lividus* Stein, 1858 (Coreidae) and *Corizus hyoscyami* (Linnaeus, 1758) (Rhopalidae). Nests are built in sandy, shaded areas and consist of the main burrow, 10–12 cm long, and one terminal cell. Males are most often found in sunny areas. Adults visit *Achillea millefolium* L., Asteraceae, as the main source of nectar.

Keywords

Behavioural ecology, digger wasps, larva, predators, parasites

Introduction

The genus *Dryudella* Spinola, 1843 is classified into the family Astatidae and comprises 58 species (Sann et al. 2018; Pulawski 2021). The genus has a cosmopolitan distribution except that it is absent from the Australian region. Currently three species are known from Poland: *Dryudella femoralis* (Mocsáry, 1877), *D. pinguis* (Dahlbom, 1832) and *D. stigma* (Panzer, 1809) (Olszewski et al. 2021a).

The biology of *Dryudella* is poorly known (Bohart and Menke 1976). Females of this genus build a single or multi-celled nest in the ground and provide it with paralysed prey. The preferred prey are nymphs of Heteroptera, mainly from the family Lygaeidae, but less frequently also Alydidae, Coreidae, Cydnidae, Pentatomidae, Reduviidae, Rhopalidae and Scutelleridae (Bohart and Menke 1976). The prey is transported in flight or on the ground. Frequently four to seven Heteroptera specimens are deposited in a cell (Kazenas 2001). During hunting, the nest entrance remains open or is temporarily closed (Kazenas 2001). The egg is laid transversely across the prosternum of the prey. The female spends the night in the nest. Cuckoo wasps of the genera *Hedychridium* Abeille de Perrin, 1878 and *Hedychrum* Latreille, 1802 (Chrysididae) and flies of the genus *Senotainia* Macquart, 1846 (family Sarcophagidae) are known as nest parasites of *Dryudella* (Kazenas 2001). Paukkunen et al. (2015) also mentioned *Holopyga* Dahlbom, 1845. Until Parker (1969) resurrected the genus from synonymy, *Dryudella* was lumped with *Astata* Latreille, 1796.

The biology of *Dryudella* was summarized by Parker (1969). Information on larval morphology was given only by Williams (1946), who provided a short description of the mature larva of *Dryudella immigrans* (Williams, 1946). The published data on *D. stigma* refer mainly to the food base of larvae (Ferton 1901; Verhoeff 1951; Lomholdt 1984), nesting habits (Nielsen 1933) and visiting flowers (Rudow 1912).

The aim of the present study is to provide the first comprehensive information on the nesting of *D. stigma* including: 1) digging the nest and transporting the prey to the nest; 2) the prey range, including species and number of individuals per nest; 3) the nest structure: determining the number of cells, length and diameter of the main burrow, length and depth of the cell and vertical section of the nest; 4) the description of the mature larva, and 5) the phenology of all stages of *D. stigma*.

Materials and methods

Our study was conducted in the town of Kowalewo Pomorskie (53°10'05.9"N, 18°52'17.6"E) in central Poland from early June to end August 2020 on sunny and warm days (with a temperature at least 18 °C). The study site was an eight m^2 home terrace covered with sand surrounded by an abandoned arable land overgrown with herbs. The dominant species growing around the study area were: *Tanacetum vulgare* L., *Taraxacum officinale* F.H. Wigg., *Geranium pusillum* L., *Trifolium arvense* L., *Lactuca serriola* L., *Cerastium holosteoides* Fr. em. Hyl., *Berteroa incana* (L.) DC., *Artemisia vulgaris* L., *Achillea millefolium* L. and *Potentilla anserina* L.

Nesting activities (i.e. digging nests and transport of the prey) were analysed from videos taken with a Canon Camera CCD-V800E 10× video camera and by direct observation. During our absence, a camera was set up in the study site so as to maintain continuity in observation as much as possible, which took place mainly between 9.00 a.m. and 15.00 p.m. An additional Raynox Macroscopic Lens M-250 was also used for the photographs. The prey range was determined by nests inspection. The structure of the nest was analysed by moistening the sand and gently digging. While the females were active (from end June to early September), their nest were dug up and their eggs, larvae and cocoons were collected for analysis. Larvae and pupae of the cleptoparasitoid digger wasps were kept in Eppendorf tubes but the cultivation under laboratory conditions from the egg stage to pupae was not successful. The durations of the larval stage of digger wasps were recorded during nest observations. The eggs and larvae were fixed in Pampel solution (30 volumes of distilled water, 15 volumes of 96% ethanol, 6 volumes of formaldehyde and 4 volumes of glacial acetic acid) as described (Švácha and Danilevsky 1987). In order to describe the morphology of larval specimens, we transferred some of the larvae into Pampel solution (rearing the remaining larvae to adults for the identification of species). After taking photographs of the intact larvae, we examined their sclerotized parts. For this purpose, we placed the larvae into 10% solution of hot (60 °C) potassium hydroxide for 12 hours to clear all parts of the body except the integument. We stained the integument in 5% Chlorazol Black E (Sigma Aldrich) for 2 seconds and moved the specimens into 96% ethanol for preservation. To observe the identification features, we placed the integument into glycerol and separately observed the head, mouthparts, spiracles, and other important parts of the integument under a light microscope. We used the same specimens for the study of small structures such as setae, sensillae, or mouthparts. We drew figures of (1) the whole body from lateral view; (2) the head with a focus on the clypeus, labrum, maxillae, and labium; (3) the mandibles in anterior view; and (4) the spiracles of larvae. Specimens of cleptoparasitic flies and prey were deposited in the Department of Ecology and Biogeography, Nicolaus Copernicus University, and larvae of *D. stigma* were deposited in the collections of University of Hradec Králové. Phenology of *D. stigma* was determined by field observations. Description of vegetation study area, and methodology is as given in the publication on *Oxybelus variegatus* (Olszewski et al. 2021b).

Results

Environmental preferences

Adult wasps were observed from June to early September in different places – males (Fig. 1A) most often on the sand in front of the house (south-west side) and females in a small sandy terrace of eight m² (building north-eastern side) (Fig. 2A). The distance between these places was about six meters. In total, 28 nests were registered during the research. Nests were at a short distance from each other (Fig. 1B, C), the smallest distance between nests being 5 cm. The entrances were open all the time. Females

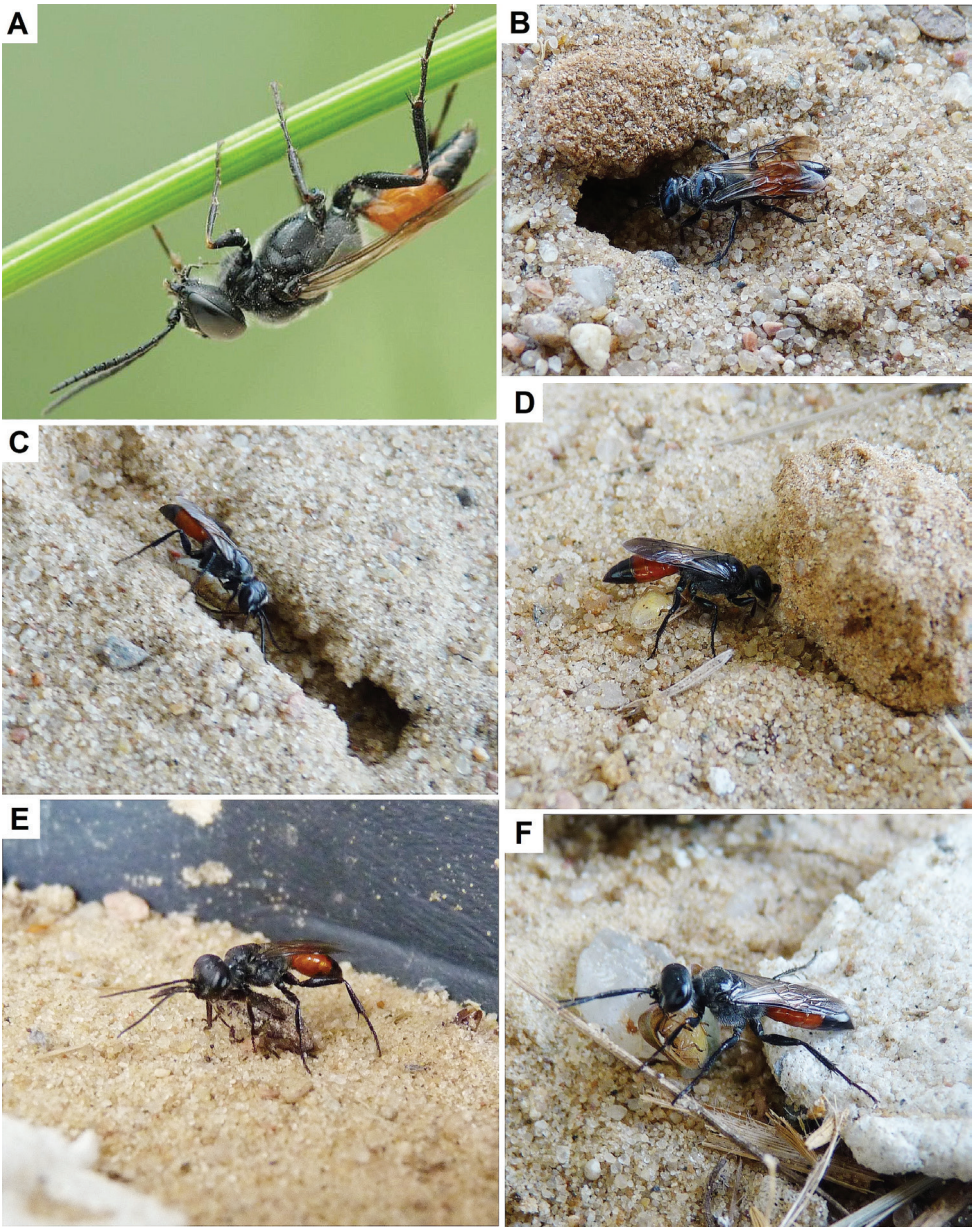

Figure 1. Adult of *Dryudella stigma* **A** male **B–F** female with prey at nest entrance.

transported bugs, supporting the prey with mandibles and legs (first pair) in flight or on the ground (alternately with small jumps) between 10.00 a.m. and 1.00 p.m. from the end of June to early August (Fig. 1C–F). The development of *D. stigma* is presented in the Fig. 4A–J. The egg stage took 2–3 days (N = 8). Egg length was 1.76 mm, and its width (maximum) 0.52 mm (N = 3) (Fig. 4A). The larval stage took 11–14 days (N = 6). The larva turned to praepupa and hibernated. The maximum number of active

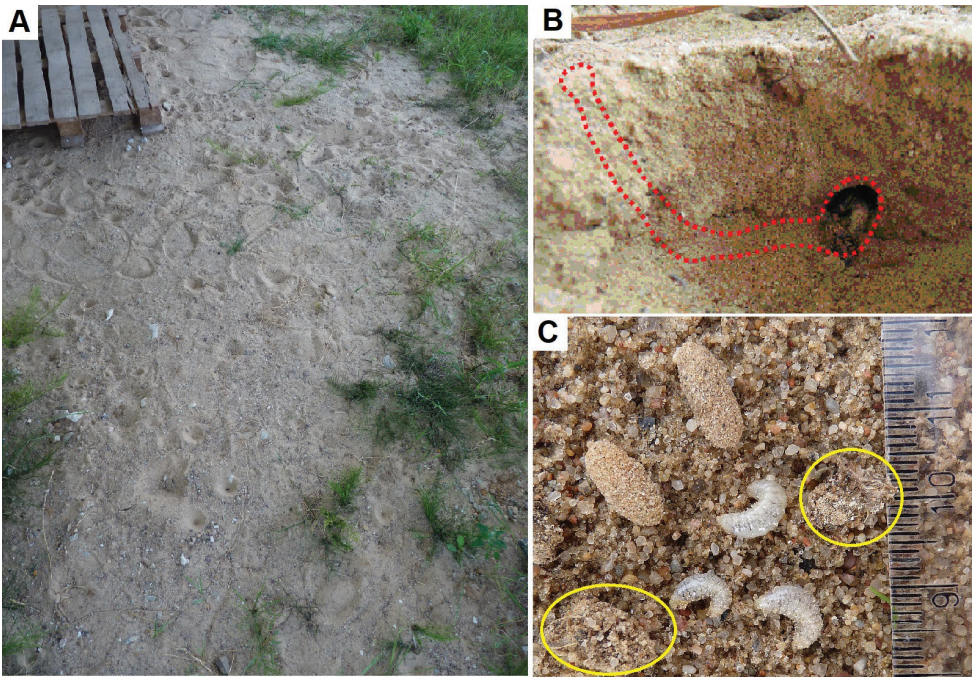

Figure 2. Nest of *Dryudella stigma* **A** place with nests **B** lateral view of nest **C** larvae and cocoons of *D. stigma* and cocoons of cuckoo wasps (yellow circles).

Table 1. Prey of *Dryudella stigma* from the eight observed nests.

Family	Species	Imago	Nymph	Number of individuals	[%] all prey
Pentatomidae	*Aelia acuminata* L.	1	39	40	83.33
Pentatomidae	*Dolycoris baccarum* L.	0	1	1	2.08
Coreidae	*Ceraleptus lividus* Stein	0	2	2	4.17
Rhopalidae	*Corizus hyoscyami* (L.)	0	5	5	10.42
Total				**48**	**100**

nests was recorded on 18th July, when 12 females transported prey to their nests during an observation period of three hours.

The nest consisted of a main burrow 10–12 cm long (with a diameter of 3.5–4 mm) inclined at a slight angle and ending in one cell (N = 2) (Fig. 2B), in which a mean of six paralyzed *Aelia acuminata* L., less often *Corizus hyoscyami* (L.), *Ceraleptus lividus* Stein and *Dolycoris baccarum* L. (Tab. 1) were deposited in a total of eight nests. During nest excavation two cocoons of cuckoo wasps were found (Fig. 2C). The cocoon of *D. stigma* (Figs 2C, 4J) was a fragile affair of silk and fine grains of sand.

Description of larva

Material examined. 5 specimens.

Diagnosis. The mature larva of *D. stigma* is similar to that of *D. immigrans*, with fusiform body and smooth cuticle, with lateral and dorsal tubercles ill-visible or absent

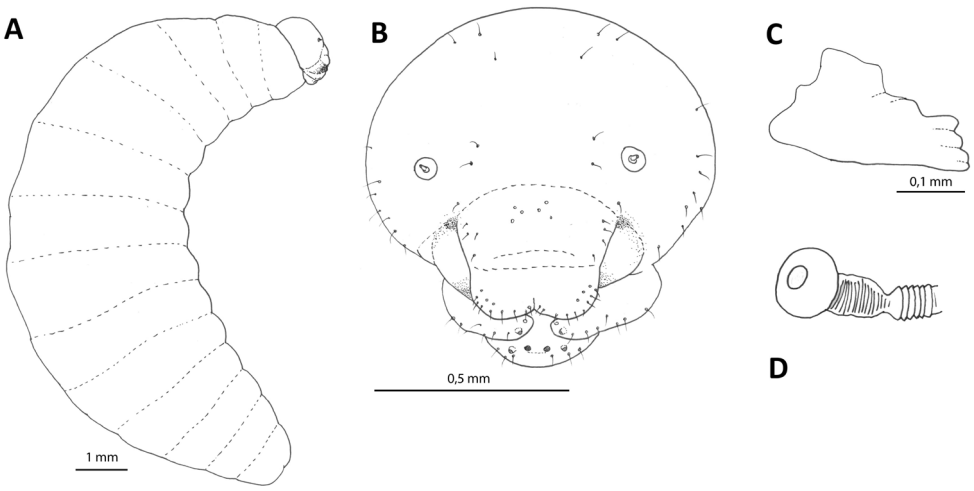

Figure 3. Larva of *D. stigma* **A** body, lateral view **B** head, frontal view **C** mandible, frontal view **D** spiracle.

(Fig. 4G–I). It is smaller than larvae of *Astata*. The mouthparts are small and not elongated (Fig. 3B), mandible is brownish and sclerotized, with four small and blunt apical teeth (Fig. 3C). All studied larvae were very similar in general appearance and did not differ chaetotaxy and morphology.

Description. Length of larvae: 8.06, 9.32, 9.92, 10.64, 11.27 mm.

Body length 8.1–11.3 mm (N = 5). Body colour cream-like (young larvae) (Fig. 4B–F) or light yellow (mature larvae) (Fig. 4G–I). Integument with very small spicules, well visible only under very high magnifications. It bears only a few slender, not elongate, pale setae, tapering to fine points, arising from small but distinct alveoli. Several setae are visible on mouthparts. Only the head and mouthparts brownish coloured in contrast to cream-like rest of body. Body form of post defecating larva fusiform, moderately wide and not dorsoventrally flattened, thoracic segments and last four abdominal segments much narrower than the other, with T2–T6 the widest (Fig. 3A). Paired body tubercles ill-developed on metasomal segments except T10, very small and inconspicuous and absent on T10. Dorsal tubercles not developed. Body shape of postdefecating larva in profile with T2–T6 having greatest diameter and outline tapering slightly forward and backward from there. Abdominal segment 9 more hirsute than previous ones, segment 10 attached to middle of segment 9 in lateral view; anus positioned medially and transverse. Spiracles (Fig. 3D) unpigmented, subequal in diameter; atrium globular, slightly wider than deep, slightly projecting above body wall, with rim; peritreme width 5 × as large as atrial opening diameter; atrial inner surface with rows of wrinkles concentric with primary tracheal opening; primary tracheal opening with collar; subatrium short, with about 10 or more chambers of approximately equal size except one or two next to atrium slightly larger in diameter. Sex characters unknown.

Head. Head moderately small in relation to body size; oriented in normal, hypognathous position relative to thorax. Setae long but sparse on upper part of head cap-

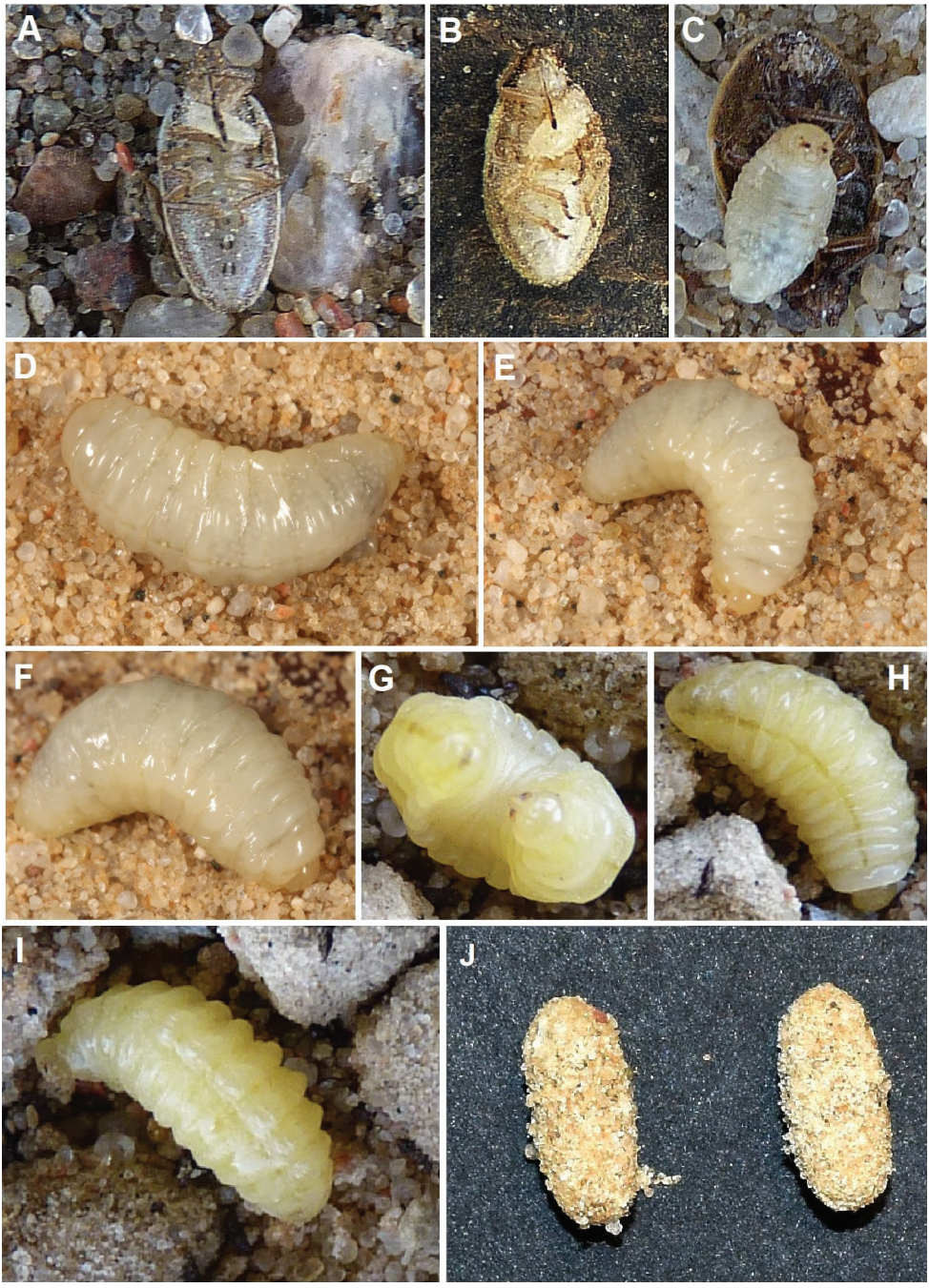

Figure 4. Development stages of *Dryudella stigma* **A** egg on prey of *Aelia acuminata* **B–I** larva **J** cocoons.

sule; those of maxillary and labial apices large, straight and conspicuous. Head capsule unpigmented except at points of articulations with mandibles; mandibles moderately pigmented except mandibular apex and articulation with head capsule conspicuously

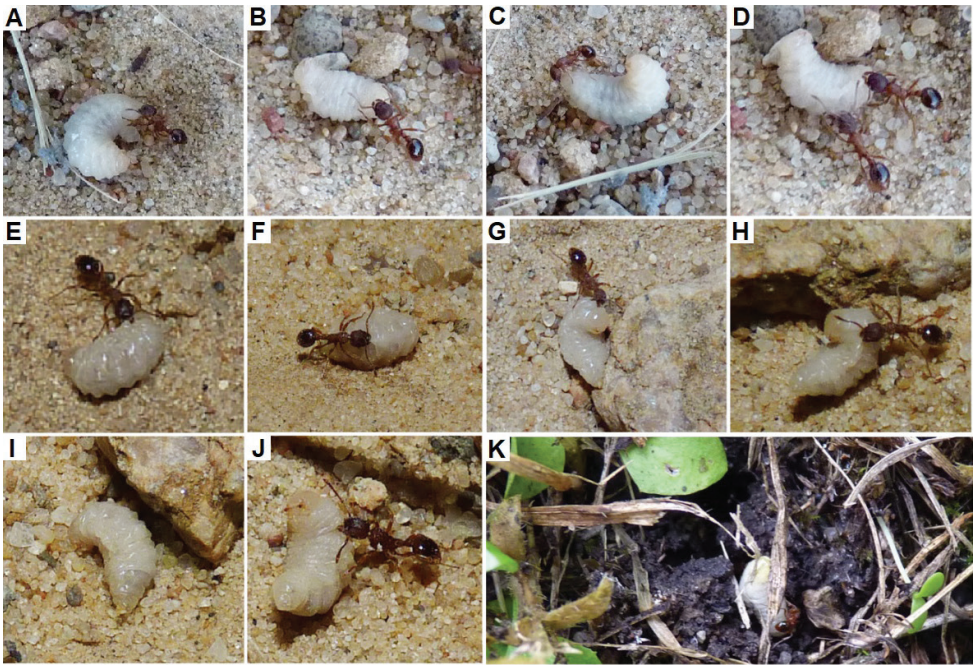

Figure 5. Interaction of larvae of *Dryudella stigma* with *Myrmica rugulosa* **A–C** feeding of *M. rugulosa* on larva secretion **D–K** transportation of the larva to the ant nest.

pigmented; maxillary sclerites faintly pigmented; salivary lips not projecting, unpigmented; antennal papilla, maxillary and labial palpi all uniformly moderately pigmented (Fig. 3B). Spiculation present but only sparse even both on hypopharynx and maxilla. Coronal and postoccipital ridges absent. Tentorium mostly absent because of impending ecdysis. Parietal bands absent. In lateral view, clypeus not projecting beyond frons, antenna arising from well-developed prominence, and labrum extending slightly beyond clypeus. Diameter of basal ring of antenna about two-thirds minimum between ring and center of anterior tentorial pit; antennal papilla distinctly but not conspicuously pigmented, moderately large and elongate, longer than one and half basal diameter, apically rounded, bearing one larger and four small sensillae apically. Frontal area between antennae with three setae laterally. Parietal region with five setae from pleurostomal ridge to front tentorial pit, and six setae above the frons on the occiput. Clypeus wide, with ill-developed basal and apical margins, and four short sensillae on each side. Labrum emarginated apicomesally, with a group of eight to nine conspicuous setae and several smaller sensillae on each side apically; labral sclerite not defined and only very poorly pigmented. Epipharynx simple, without any visible structures. Mandible moderately robust but narrowing toward apex; darkly pigmented, with four small apical teeth and one lateral tooth, with three apical teeth longest and lateral tooth smaller and blunt (Fig. 3C); cuspal area developed, projecting, with surface irregularly uneven; outer mandibular surface asetose. Maxillary apex strongly bent mesad in frontal view, maxillary palpus looking subapical; cardo distinct, poste-

rior end directed toward posterior tentorial pit; stipes weakly sclerotized; maxillary palpus elongate, less than two times basal diameter, pigmented like antennal papilla but slightly thinner than papilla. Stipes with seven conspicuous setae. Labium not divided into prementum and postmentum; apex moderately narrow in frontal view; premental sclerite apparently absent as well as border between pre- and postmentum. Three setae on both sides and two smaller on ventral surface of labium. Salivary lips round and well visible, with inner surface bearing parallel longitudinal grooves; width of lips slightly more than twice width of maxillary palpus. Labial palpus moderately elongated, about as long as wide, with three sensillae in middle.

Discussion

Females of *Dryudella stigma* hunt various species of Hemiptera of the families Lygaeidae, Scutelleridae, and Pentatomidae as prey for their larvae (Ferton 1901; Verhoeff 1951; Lomholdt 1984), while probably selecting the most numerous prey at their nesting locality (*A. acuminata* in our case). For other species, various authors recorded a wide spectrum of prey species. Verhoeff (1951) lists *Palomena prasina* (Linnaeus, 1761) as prey of *D. freygessneri*. Ferton (1901) lists larvae of *Emblethis griseus* (Wolff, 1802) as prey of *D. stigma* (but determination of the host from Algeria is certainly incorrect: the species does not occur in North Africa) and Verhoeff (1951) lists other Heteroptera: *Phimodera humeralis* (Dalman, 1823), *Sciocoris cursitans* (Fabricius, 1794). Lomholdt (1984) adds *Drymus sylvaticus* (Fabricius, 1775) and records the nest parasite – *Hedychridium roseum* (Rossi, 1790) (Chrysididae).

Ferton (1901, 1908) lists immatures of *Aphanus* sp. and *Emblethis verbasci* (Fabricius, 1803) as prey of *D. tricolor*. According to Verhoeff (1951), females of *D. pinguis* hunt on larvae of Heteroptera such as: *Trapezonotus arenarius* (Linnaeus, 1758), nymphs (probably) of *Nysius thymi* (Wolff, 1804), and *D. sylvaticus* Fabricius, 1775. Lomholdt (1984), add *Rhyparochromus pini* (Linnaeus, 1758). The same author also notes that this species digs its nests on sandy soil in sunny places, usually on small cliffs, along the shore of water reservoirs.

In this study, we add as prey of *D. stigma*: *Aelia acuminata* (Pentatomidae), *Ceraleptus lividus* (Coreidae) and *Corizus hyoscyami* (Rhopalidae), while members of Coreidae and Rhopalidae are recorded as a prey of *Dryudella* for the first time (Table 1).

The activity of the males on the opposite side of the building coincided in part with the observations by Evans (1958), who observed *Astata unicolor* Say, 1824 in his garden from July 29 to August 17.

We have recorded the females active in a quite short-day period and probably the choice of the place by the females to build the nest was related to the appropriate daytimes (the area shaded from noon). Shaded places on sandy ground may be associated with an appropriate soil temperature and a smaller number of nest parasites. The observed period of females activity during cell provisioning were similar to those observed by Blösch (2000), who registered a female of *D. pinguis* on June 1, 1994, transporting five larvae of Heteroptera between 11.30 and 12.30 p.m. Evans (1963) reported that

females of the North American species *Dryudella montana* (Cresson, 1881) transported prey to the nest about noon on July 30.

The fact that *D. stigma* can inhabit new (highly anthropogenic) environments is a known phenomenon, but after a few years population levels decline (Witt 1997).

The cuckoo wasp *Hedychridium roseum* (Rossi, 1790) is a nest parasite of *D. stigma* (Lomholdt, 1984). During the video analysis and observation, no cuckoo wasps were observed near the nests of *D. stigma*, but larvae parasites of unidentified cuckoo wasps were found in the cells. The biology of this chrysidid may be similar to *Holopyga*, which is known to place eggs on Heteroptera, and the wasps carry the egg together with the prey into the nest (Veenendaal 2012). According to the last published data *Holopyga generosa* (Foerster, 1853) is nest parasite for a closely related species *Astata boops* (Schrank, 1781) according to Veenendaal (2012). During one of the observations, ants *Myrmica rugulosa* F. Smith, 1858 transporting a larva *D. stigma* to the anthill were recorded. An ant was feeding on the secretions from the last segment of the larva (Fig. 5A–K).

The larva of *D. stigma* compared to *D. immigrans* at least when it is mature, does not show any setae, except for the mouth region. The body is slightly modified, has no lateral thoracic papillae and in the lateral view, the dorsal segments are not distinct which agrees with the description by Williams (1946). With the exception of Evans (1958), published descriptions of larvae of Astatinae are very short and incomplete and usually lack drawings of the whole body, head and mouthparts. We can then only suppose that the larva of *D. stigma* resembles in its morphology the species of *Astata*. Evans (1958) provided a comprehensive description of *A. unicolor*, which differs in the size and in positions and shape of the mandibular teeth.

Conclusions

Females of *D. stigma* usually provision their brood cells between 11.00 a.m and 13.00 p.m. The preferred prey were *Aelia acuminata*, *Dolycoris baccarum*, *Ceraleptus lividus* and *Corizus hyoscyami*, the former one being the most abundant. Female of *D. stigma* transported bugs, supporting the prey with mandibles and legs (first pair). The nest main burrow is practically oblique along its length, leading to one or two cells. The entrance to the main burrow is always open during the provisioning period. The egg is laid transversely across on the prosternum of the prey. The mature larva of *D. stigma* is similar to other larvae of this genus and of the related genus *Astata*, with fusiform body with smooth cuticle with lateral and dorsal tubercles only ill-visible or absent, differing from the larvae of the relatives by the size and shape and positioning of mandibular teeth.

It is smaller than larvae of the related genus *Astata*. The mouthparts are small and not elongated, mandibles are brownish and sclerotized, with four small and blunt apical teeth. All five studied larvae were very similar in general appearance and did not differ in chaetotaxy and morphology.

Our research on *D. stigma* reveals its role as a predator of some species that can be crop pests, such as *Aelia acuminata.*

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