Notes on the biology of Dasypogon diadema (Fabricius, 1781) (Diptera: Asilidae)

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Abstract: Dasypogon diadema (Fabricius, 1781) was studied intensively in 1995 in an area west of Darmstadt, Germany. Its behaviour, especially the method of oviposition, is recorded. The eggs are laid in clutches in the soil, each protected in a sand "cocoon", a phenomenon which has previously been recorded only in Antipalus varipes (Meigen, 1820) among the Asilidae.

Key words: Diptera, Asilidae, Dasypogon diadema, biology

Introduction

Although *Dasypogon diadema* (Fabricius, 1781) is one of the most common robber flies in Central Europe, relatively little is known about its biology. It is a large and sexual dimorphic species. The males have a black abdomen and blackish wings, the females have a black abdomen with red markings, brownish wings and are usually somewhat bigger (Fig. 1). Some new observations about its biology, especially its oviposition, are described in this paper.

Study site and methods

Dasypogon diadema was studied intensively during the period of summer 1995 in an area west of Darmstadt, Germany (49°51'N, 8°36'E) which was formerly part of a sand-dune area in the upper valley of the river Rhine (Oberrheintalgraben). The area covers about 30 hectares at an alitude of about 110 m and is currently used by the army as a training area. It is surrounded by two motorways (NE and NW) and a Federal Highway in the south.

The surface layer was removed during the 1930th so that the present top soil contains more lime than the neighbouring areas. The area covers a gradation of different plant communities: the peripheral zone and the central part are overgrown with pine trees, the greater part with a dense cover of *Phleum arenarium* (sand cat's-tail) but a mosaic of open patches is present (Fig. 2). CEZANNE (1983) reports approximately 200 higher plants from these patches. A lot of paths run through the area, which contribute to the preservation of sandy places.

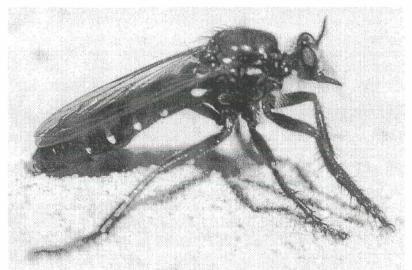


Fig. 1: Dasypogon diadema, female, foraging position on the ground.

D. diadema is common in the Mediterranean region but appears also locally in Germany. It inhabits areas of sparse plant cover in the upper valley of the Rhine and was also found in north-eastern regions of Germany in the last century. The complete distribution is unclear since WEINBERG (1979, 1985, 1986, 1987, 1989, 1991) has described additional species from the western and eastern mediterranean region which resemble *D. diadema*.

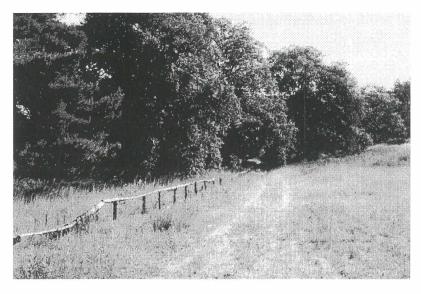


Fig. 2: Southern border of the army training area in Darmstadt.

Flies were observed and counted over the entire area and notes were made of sex and behaviour. Some studies were performed in the laboratory and some of the described behaviour was recorded by using a video camera.

Other asilids recorded in this area between April and late August 1995 include Antipalus varipes (Meigen, 1820), Choerades ignea (Meigen, 1820), Cyrtopogon lateralis (Fallén, 1814), Dioctria atricapilla Meigen, 1804, Dysmachus trigonus (Meigen, 1804), Eutolmus rufibarbis (Meigen, 1820), Holopogon fumipennis (Meigen, 1820), Lasiopogon cinctus (Fabricius, 1781), Leptogaster cylindrica (De Geer, 1776), Machimus rusticus (Meigen, 1820), Neoitamus socius (Loew, 1871), Neomochtherus geniculatus (Meigen, 1820), Philonicus albiceps (Meigen, 1820), Stichopogon elegantulus (Wiedemann in Meigen, 1820), Tolmerus atricapillus (Fallén, 1814), Tolmerus cingulatus (Fabricius, 1781) and Tolmerus pyragra (Zeller, 1840).

Results and Discussion

Distribution

Dasypogon diadema was first described from Italy and is known from France, Germany, Greece, Spain and the former Yugoslavia. Records from other countries must be rechecked to eliminate the new species described by WEINBERG (1979 - 1991). Existing studies show that D. diadema is the most common species of the diadema-group in Europe and predominantly inhabits the central region of the Northern Mediterranean. Its northern border is situated in the central part of Germany. The following German records are known: JAENNICKE (1868) from Eberstadt and Jugenheim (Bergstraße), KITTEL & KRIECHBAUMER (1868) from Nürnberg, Regensburg and the Bavarian mountains, NEUHAUS (1886) from the Mark Brandenburg, SACK (1907) from Auerbach and Jugenheim, RAPP (1942) from the Höllental and Halle (Saale), MIKSCH et al. (1993) from Schwetzingen and Darmstadt and GELLER-GRIMM (1996) from Darmstadt, Eberstadt, Griesheim and Viernheim. Three records have not previously been published: Frankfurt/Oder, without date, RIEDEL leg., 1 female [Museum Darmstadt, HLHD]; Lampertheimer Heide (north of Mannheim, 49°36'N, 8°32'E), 04.07.1995, BATHON leg., several specimens [pers. comm.] and Dudenhofen (east of Speyer, 49°20'N 8°24'E), 09.07.1995, BETTAG & GELLER-GRIMM leg., 1 male.

It appears from the above that the current distribution is limited to the upper valley of the Rhine, where the soil is mainly sandy and the temperature is normally the highest in Germany.

Habitat

D. diadema is common in Southern Europe, where it inhabits different habitats. ADAMOVIč (1971a, b) found it on steppes, partly eroded hilly slopes, sandy hollows, weedy grass plots, Christ's thorn shikara and on grassy foothills. CLOUDSLEY-THOMPSON (1960) found it on dunes at the Atlantic coast. The author has found it also in dry meadows, pastures, olive groves, and clearings in Southern France and the Alps. The more adverse climate in Germany restricts its distribution to xerothermous places, which are present in the upper valley of the Rhine. In addition the soil must be sandy to facilitate oviposition. *D. diadema* is therefore usually found in former sand-dune areas (a result of the last glacial period). Most

of these have been destroyed by agriculture and development during the present century.

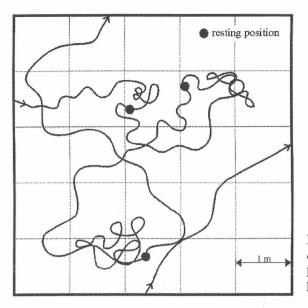


Fig. 3: *Dasypogon diadema*, flight path and resting position of a male.

D. diadema is found mainly on the open areas at Darmstadt, usually on bare patches or somewhat overgrazed areas. During the midday heat some specimens (mainly males) can also be found in wooded areas. The temperature rose above 44°C on soil (3 p.m., 8 July 1995), 36°C in the shadow, and 33°C inside the vegetation (10 cm above the ground). The flies could therefore be frequently observed inside the vegetation.

Seasonal Occurrence and Abundance

The imagines were found during the period between June 26 and August 3, 1995. The first specimens flew in the southern area near the forest edges on the last days in June, when the climate was most favourable in this area. Their abundance afterwards increased to a maximum during the period between June 30 and July 20. At this time, *D. diadema* could be found in all open areas; usually at a density of about 1 specimen per 10 square metres.

Diurnal Activity and Behaviour

The first males flew as early as 9 a.m., whereas the females usually showed their first activity at 10 a.m. During the midday heat the flight activity of both sexes decreased. Activity also decreased in the late afternoon (after 6 p.m.). After 8 p.m. no activity could be observed; the flies hung on stems of flowers and grasses or under leaves, where they stayed overnight. On cloudy days the first activity did not start until 10.30 a.m. and did not decrease during the midday period. *D. diadema* otherwise showed the same behaviour on such days, in contrast to other species which were less active. No distinction could be made between times of sexual activity and times of hunting. Oviposition was observed exclusively before midday.



Fig. 4: Dasypogon diadema, mating (left: female, right: male).

Foraging Positions

The foraging behaviour of males was quite different from that of females. The former usually stayed no longer on the ground or on stems than 5 - 10 sec., they otherwise showed a constant migratory restlessness, primarily aimed at the discovery of females. They also searched for prey during their flights and captured their victims in the air. These scouting flights lasted for about 5 - 15 m on average (sometimes more than 200 m) and 30 - 60 cm above the ground. The direction of the flights changed constantly and the area was extensively reconnoitred during these patrols (Fig. 3). MUSSO (1972) also describes this behaviour. The females were more territorial, staying for longer times at their foraging position (usually facing upwards on stems, sometimes on the ground). They only flew if they saw potential prey or if they were disturbed (mostly by males).

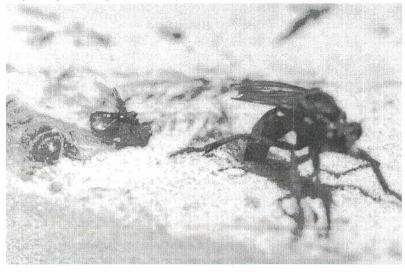


Fig. 5: *Dasypogon diadema*, beginning of an oviposition [video recorded]. (The blur of the picture is caused by the continuous trembling of the female during its activity.)

Prey Selection Methods

The males usually flew over the area and rested on the ground for only short periods. Prey was usually captured in flight; on only four occasions was a single male observed to attack potential prey from the ground. The flying males typically changed their direction if other insects crossed their flight path within a maximum distance of 2 m. They then captured the prey in mid-air using all six legs, killing them immediately or following a short struggle on the ground after falling together. If another male approached the hunting male in the air, the latter flew close, but did not touch him. Both would fly parallel at a short distance for some seconds before flying off in different directions. In only one case were both males observed to touch, separating after a short struggle. The females foraged mainly from vegetation, seldom from the ground. They perched head upwards on stems of flowers and grasses in open areas, turning their heads to follow the flight of potential prey. When one was identified, they quickly turned their bodies and flew towards it. The females also captured their victim using all legs and either fell or flew to the ground with it. The predator then usually laid on its side, manipulated the victim skilfully with its legs and killed it by piercing the thorax. One female was observed to successfully complete 54 out of 63 darting capture flights. When the temperature increased, especially at midday, the flies flew with their prey into the vegetation to find shadow.

The behaviour of the females can be summarized as follows: 1. Optical fixation by movement of the head. - 2. Alignment of the body towards the victim. - 3. Darting flight. - 4. Capturing in the air. - 5. Landing on ground. - 5. Manipulation with the legs. - 6. Killing by piercing. - 7. Transport of the victim (on some occasions). - 8. Sucking out and occasional manipulation.

Choice of Prey

POULTON (1906), TIMON-DAVID (1953), ADAMOVIč (1963a, b, 1966, 1972) and MUSSO (1970) have previously described the prey of *D. diadema*. The results of this study agree with their results. *D. diadema* is distinctly stenophagic, more than 70 percent of the prey being Hymenoptera. The species is also a significant predator of *Apis mellifera*.

Apis mellifera was rare in Darmstadt during the study period, the abundant Hymenoptera being species of *Bombus*. That is possibly the reason why, out of 308 prey records, 84 percent were *Bombus* spp. and 16 percent were species of *Andrena*, *Megachile*, *Paravespula* and *Apis mellifera*. Females were observed more frequently than males with prey (178 of 308 records). Feeding usually took place from a hanging position and manipulation was frequent, usually five or six times during which the point of insertion of the hypopharynx changed (thorax - abdomen - head - thorax and so on). The duration of the sucking period was 44 min. on average for a *Bombus* spp. (minimum: 28, maximum: 187 min.). Abdominal

pumping was observed during feeding, but also during and after high activity (flight, at times of highest temperature, or oviposition). *D. diadema* is excellently well-adapted for struggling with Aculeata species with its long and thin legs, strong spur at the apex of the fore tibia and long proboscis. These features are important adaptations to the dangerous prey.

Courtship Behaviour and Copulation

POULTON (1906) describes the courtship behaviour from a location in Spain, where a male "flew nearer to the female. Although only three or four inches away, he did not walk but flew towards her, taking up a nearer position, in which he sometimes faced her from the side, sometimes from behind. On one occasion he alighted only an inch behind the female. The only movements observed in the female after alighting were of the head, but the male often fluttered his wings." In contrast to this description no courtship behaviour was recorded during the present study, neither in Darmstadt nor in the laboratory. This is not a contradiction because other studies show (LAVIGNE & HOLLAND 1969, GELLER-GRIMM 1995) that some species are variable in their behaviour and can adapt according to the situation. The males approached the females directly on the ground or in the air after they identified them during their searching flights.

Mating was initiated after a short struggle. Sometimes the female escaped from the male's grasp and flew away. Otherwise the male curled his abdomen between his legs, his genital claspers grasped the female's ovipositor and union was accomplished. The male then relaxed his grip and fell back, the final mating position being end-to-end. The female then flew up to find a better place. She decided the direction of the flight, the male staying motionless and hanging downwards, sometimes beating his wings. They usually landed on a stem or on grass (Fig. 4) and stayed motionless for a long period of time. If they were disturbed, they would fly away to another place or terminate the mating. The average time in copula was 55 min. (minimum: 25, maximum: 78 min.). POULTON (1906) describes a duration of only 6 min. Approximately 10 min. before mating finished, the female became somewhat restless and touched the male's abdomen with her hind legs. POULTON (1906) also records cannibalism, but this behaviour was not observed during the present study. It was only observed in closed glass containers in the laboratory. It is surprising that cannibalism was not recorded because intraspecific contact, especially between different males or between the two sexes is frequent. They must have a well-developed sense for the distinguishing between prey and members of their own species in a short space of time. Robber flies have a keen optical sense and it may be significant that *D. diadema* is a sexually dimorphic species. LAVIGNE & HOLLAND (1969) analysed the function of wing sound for 7 species in Wyoming, but no observable reaction could be discerned in any of the tests (before mating). A meeting of two males of *D. diadema* in the air occurs without direct contact, so olfactory recognition is improbable.

Oviposition

The behaviour of the females changed distinctly before and during the oviposition. They became more active, frequently flew up for short distances, and ran over the sandy soil between the vegetation. Their wings were spread and vibrated frequently, abdominal pumping was also sometimes observed. The females trailed their ovipositor across the ground and frequently stuck them into the soil. As soon as a female found a suitable place, she rapidly moved the ovipositor around, curled her abdomen under herself, and pushed the blunt ovipositor down into the soil (Fig. 5). The ovipositor was normally sunk to the full depth of the abdominal length less the first and second segments. As the abdomen was pushed so deep that the wing tips touched the ground, the wings were spread. The tip of ovipositor therefore reached a depth of 10-13 mm at which time the female stiffened for 5 - 10 sec., with spread wings and legs. At this she vibrated her abdomen and withdrew it. Finally she smoothed the surface with her ovipositor and flew away, often to select another site for further egg deposition. In the meantime (2 min. on average) she sometimes excreted a milky and yellowish liquid. After the female had repeated her oviposition several times, she rested for a longer period of time. The oviposition of a female which had copulated two days before was recorded in the laboratory.

The results are summarized in the following table:

Date [July 1995]	Abs. time [p.m.]	Duration [min.]	Number of ovipositions
1	1:50	20	11
	2:52	25	13
2	3:15	28	8
3	5:10	29	6
	6:30	22	5
	8:40	14	4
4	4:42	19	5
	6:34	11	4

Table I. Oviposition in the laboratory

Table I. shows that *D. diadema* deposited her eggs (or "cocoons", see next paragraph) at regular time intervals, which were interrupted by longer periods and that the frequency of ovipositions decreased over a period of days. Field observations were also made, but it was impossible to follow the females for a long period of time. Oviposition was observed between 11 a.m. and 7:20 p.m. in Darmstadt. Eggs were usually deposited in shaded areas, both in the field and in the laboratory.

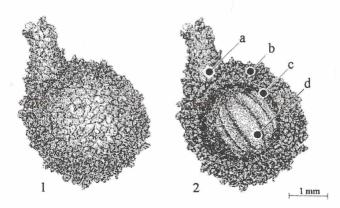


Fig. 6: Sand container or "cocoon" for the eggs.

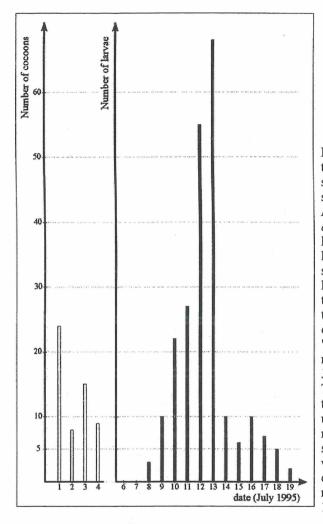


Fig. 7: Oviposiand first tion stage larvae of a specimen of Dasypogon diadema the in laboratory (collected in Darmstadt 1995). The left portion of the figure shows the number of collected sand "cocoons" during the period July 1st – 4^{th} The right portion of the figgives the ure number of first larvae, stage which emerged during the period July 8th 19^{th}

Eggs

A search for eggs deposited in the sand produced interesting sand balls at each place of oviposition (Fig. 6.1). These sandy objects have an average diameter of 4.5 mm and are tapered on the upper side (Fig. 6.2a). The outer surface is made of 3-5 layers of sand grains, which are fixed strongly with an unknown glue (Fig. 6.2b). Only the sand grains of the projection on the upper surface are loosely attached and detach easily at the base. The inside of this sand container is covered with a silky lining (Fig. 6.2c) and an average of 5 eggs is deposited in the centre (minimum: 1, maximum: 6). These eggs are white, long-oval, with a smooth surface and lined up towards the upper projection (Fig. 6.2d). The glue cementing the sand grains is certainly different from normal excrement, which is yellowish and does not adhere to sand grains.

Creation of such sand containers, or "cocoons" was first described in the case of *Antipalus varipes* (MEIGEN, 1820) by MUSSO (1981). There are some differences between the two: the sand "cocoon" of *A. varipes* encloses only one egg and has no lining. The outer layer of sand grains is missing along one longitudinal side of the egg.

MUSSO (1981) also observes that certain Bombyliidae have a perivaginal pouch in which they cover their eggs with sand., first described by SCHREMMER (1964) as "Sandkammer". ZAITZEV (1989) called these Bombyliidae the Psammophoridea group. The ovipositor of *A. varipes* is of an unusual shape for the subfamily Asilinae, whereas *D. diadema* (subfamily Dasypogoninae) has an normal ovipositor with acanthophrites. It is not known if the sand "cocoon" is produced before the oviposition, but the short oviposition time (5-10 sec.) makes this probable. It is speculated that the function of these sand "cocoons" is the protection of the eggs from the high temperature (which can be as high as $38^{\circ}C$ at 1 cm below the surface) and the dryness. In addition they provide a camouflage which protects them from predators.

Larvae

Only a late stage (possibly the third) larva and the pupa have currently been decribed (MUSSO 1978). He found the larva sucking out a Scarabaeid larva. Samples of soil from Darmstadt were checked with the aid of a sieve, but no larvae could be found. Nevertheless it proved possible to breed the first stage larvae from sand "cocoons" collected after deposition by a female on July 1st - 4th. After four days the first stage larvae started emerging from the sand "cocoons" at the base of the projection. It is not known at what time they left the eggs inside the "cocoon". Fig. 7 shows emergence data. There was a distinct peak in emergence about 12 days after the first oviposition and all sand "cocoons" were vacated by the 19th day. The first stage larvae were kept alive another 12 days, but unfortunately it was impossible to find a suitable food supply for them.

The study of the biology of *Dasypogon diadema* is not yet complete, but the observations to date indicate a high degree of adaption to their living environment and food.

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Kollegenkontakte

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Für eine monographische Bearbeitung der türkischen Cicindeliden im Rahmen einer Promotionsarbeit suche ich noch Fundortmeldungen sowie Belegmaterial (Einzeltiere und Serien) aller Arten aus der Türkei sowie benachbarter Regionen (z. B. Bulgarien, Griechenland, Zypern, Kaukasus), besonders *C. campestris*-Komplex.

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