MATING BEHAVIOUR IN DONACIINAE (COLEOPTERA, CHRYSOMELIDAE)

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Abstract

The mating behaviour in 14 Palaearctic species of Donaciinae was studied in captivity. A preliminary stage is separated within the mating in 12 species. During this stage the male occupies a position on the female's elytra, but does not attempt to copulate for a long time. Precopulatory courtship is observed during the preliminary stage in nine species: male rubs female's antennal or vertex calli with his fore-tarsi. During the copulation the males of 10 species perform a courtship: they rub the female's antennal or vertex calli, or behind the eyes, or pronotum with their fore tarsi. A courtship by the rubbing of head is reported for the first time in the Coleoptera. Well developed convex vertex calli are present only in some of the species, in which the courtship by rubbing of them occurs. The position and behaviour of the male during the mating is described for each species in detail. Females of several species can feed or move here and there during the mating. At the end of mating a male usually leaves a female without the prior attempts by the female to drive him away. A female rarely pulls off a male with her hind tarsi.

Introduction

The reproductive behaviour in insects is of special interest and is intensively studied presently. A knowledge of reproductive peculiarities provides additional insights into the phylogeny as demonstrated, for example, in Orthoptera (Alexander, 1964) and scarabaeine beetles (Halffter & Edmonds, 1982). Secondary sexual characters are of a great value in a systematics. The mating behaviour of leaf beetles is characterized by a great diversity (Eberhard, 1991, 1994, Medvedev & Pavlov, 1985, 1987, Michelsen, 1963, 1966). As regards Donaciinae, this question has been studied extremely poorly. Olsoufieff (1903) noted that two or three males of *Donacia fennica* (Paykull) position themselves alongside the mating pair and patiently wait their turn. Wesenberg-Lund (1943) mentioned that males of *D. crassipes* Fabricius and *D. cinerea* Herbst actively pursue females on leaves of their host plants. Michelsen (1963, 1966) in articles devoted to the mating of long-horned beetles (Cerambycidae) dealt briefly with the separate phases of copulation behaviour in *D. aquatica* (Linnaeus). Medvedev & Pavlov (1985) described a search behaviour of the males in *D. crassipes* and *D. marginata* Hoppe. Medvedev & Pavlov (1987) observed a copulation act in *D. marginata*.

Material and methods

The observation of the mating behaviour has been performed in the captivity. Beetles were captured in the Moscow region at Glubokoe lake (23 km west of Zwenigorod) and at small

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neighbouring waterbodies (ponds, swamps and ditches) in 1995-1998. I investigated the reproductive behaviour in 14 species of *Donacia* and *Plateumaris*. I usually placed from one to four pairs of one species in a petri dish provided with leaves, stems and flowers of the host plant. The petri dishes were protected from sunlight. I studied the behaviour of beetles under the stereoscopic microscope at 8-16 x magnification through the transparent cover of the dish. The results obtained in laboratory were supplemented by field observations. The terms "antennal calli" and "vertex calli" of the head and the "anterolateral calli" of the pronotum are used after Askevold (1991).

Results

Behaviour prior to mating

During the flight period the adults of a number of Donaciinae species occur in abundance on their host plants. Therefore, a meeting of sexes is easy. On account of this I failed to observe a search behaviour in nature. Medvedev & Pavlov (1985) noted that males of *D. crassipes* raise themselves on their fore and middle legs above the surface of floating leaves of water lily and usually orientate themselves against the wind. In this position the beetle turns forward, raises and separates its antennae. These authors suggested that the males use olfactory information from the females (pheromones of Donaciinae are still unknown). However, I registered this behaviour in the both sexes. I did not observe an aggressive behaviour of the males either in captivity, or in the field. However, a single male, which meets a mating pair, usually attempts to perch upward and disturbs the copulating animals. As a result the copulation is often interrupted.

Mating

The majority of Donaciinae species usually copulate openly on the leaves and stems of their host plants. Mating individuals of *D. clavipes* Fabricius crawl foremost into the leaf axils of *Phragmites australis*. The length of the mating period was measured as 12-25 minutes for *D. marginata* by Medvedev & Pavlov (1987), and about 15 minutes for *D. cinerea* by me. When a male meets a female, he perches on her elytra from behind. The male always orientates itself immediately rightly. The antennae of the both partners are directed forward and separated. The males of *D. bicolor* Zschach and *D. brevitarsis* Thomson alternately hit the outer sides of the females antennae with their antennae during the initial period of mating. The same action takes place during the copulation act in *D. sparganii* Ahrens and when the female attempts to drive the male away in different species. I recognize a preliminary stage in the mating process in Donaciinae. The males of 12 species do not set about copulation immediately they get into position on the elytra of the female, and the aedeagus is still hidden. In addition, the males of nine of these species perform a precopulatory courtship. In all species examined, a courtship implies that the male rubs the antennal or vertex calli of the female with his fore-tarsi alternately. Males of *D. thalassina* Germar, *D. sparganii* and *D. bicolor* execute these motions continuously, others do it now and then. The position of the male on the female elytra differs during the preliminary stage and the copulation act in six species. The importance of the preliminary stage to the suc-

cessful copulation is confirmed by the following observation. One male of *D. brevitarsis* attempted to copulate without a precopulatory courtship. The female clasped the male elytra with her hind tarsi and tried to pull him off backwards. The male held on to the female strongly, but could not copulate in this position. Alternatively, beetles of *D. cinerea* and D. *vulgaris* Zschach always copulate without a preliminary stage, and females usually do not interfere with the copulation. I observed the both types of mating, with the preliminary stage and without it, in *D. crassipes*. During copulation the male of the majority of species extends to rub female's head or anterolateral calli of the pronotum. The male of *D. bicolor* rubs the female's vertex calli continuously during copulation, while others, including *D. sparganii* and *D. thalassina* perform this courtship now and then. Males of *D. vulgaris* and *D. cinerea* perform a similar copulatory courtship. The rubbing of the head as a variation of the copulatory courtship is found in the Coleoptera for the first time. It was recently pointed out that beetle males from different families rub the female elytra, thorax, femora and pygidium, or hit the antennae with his fore-tarsi (Eberhard, 1994). I have examined vertex relief in detail in the females of all the species observed and found that well developed vertex calli present in some of the species, in which a courtship by rubbing of them occurs. I have never found convex calli in the species, in which the male tarsi do not touch the female head. This suggests that the courtship behaviour was primary and respective morphological structures arose as a result of the sexual selection. It is interesting to note that the shape of vertex and pronotal calli are used as taxonomic characters for the *Donacia* and *Plateumaris* species (Medvedev, 1965, Lopatin, 1986, Lopatin & Kulenova, 1986, Askevold, 1991). However, a function for these calli in the females during a mating was not known before. A function of the male middle and hind legs is to maintain the mating position.

Table 1. Shape of vertex calli in females of some Donaciinae species.

Species	Male rubs calli	shape of calli	number of specimens
Donacia			
aquatica	+	C,W	10
bicolor	+	C	10
brevitarsis	+	W,A	10
cinerea	+	W	8
clavipes	–	W	10
crassipes	+	C,W	10
*dentata**	–	C,W	10
obscura	+	C,W	4
simplex	+	W	10
sparganii	+	C	9
thalassina	+	C	9
versicolorea	–	W	8
vulgaris	–	W	10
Plateumaris discolor	–	A	10

+ = yes; – = no. Shape of vertex tubercles: C = convex; W = weak; A = absent. *male rubs antennal calli.

Position and behaviour of male in different species during the mating

Donacia aquatica (Linnaeus)
Mating was observed in two pairs. The male performs the same behaviour during the preliminary stage and copulation act. He weakly rubs vertex calli of female with fore-tarsi; his middle legs clasp her body laterally, with tarsi resting between the middle and hind coxae, or in front of the middle coxae; his hind legs rest on substratum. Michelsen (1963) described another facet of the courtship in this species: the male strikes the female's body with his antennae.

Donacia bicolor Zschach
The preliminary stage and copulation act were observed in eight and four pairs, respectively. The male occupies the same position during the preliminary stage and copulation act. The male rubs female's vertex calli with fore-tarsi. His middle legs clasp her humeri at the front, with the middle tarsi placed between fore and middle coxae or behind the latter, hind tarsi rest on the substratum behind the female when she is motionless, and clasp her abdomen or drag behind when she crawls.

Donacia brevitarsis Thomson
The preliminary stage and copulation act were observed in 12 and eight pairs, respectively. The position of the male during the preliminary stage and copulation act does not differ. The male puts his fore-tarsal segments 2-4 or 3-4 on the female's head between the eyes and sometimes rubs the vertex calli, segment 1 or 1-2 on her pronotum interior to the anterolateral calli. His middle legs clasp her humerae at the front, with tarsi meeting or crossing on the metasternum, his hind legs clasp her abdomen, with tarsi crossing or turning forward.

Donacia cinerea Herbst
The preliminary stage was not found, although 12 pairs were under my observation. During copulation the male puts his fore-tarsi laterally on the female's pronotum with an inclination in front and down or dorsally interior to the anterolateral calli. In some cases the fore-tarsi are placed asymmetrically: one laterally and the other dorsally on the pronotum or on the head of the female. The male rubs the female's head below the eyes, the vertex calli or anterolateral calli of the pronotum now and then. His middle legs clasp the female's body laterally, with the tarsi placed between the middle and hind coxae, or on the elytral epipleura above the hind coxae. The male hind legs rest on substratum behind the female elytral apex or are brought together over her abdominal sternites.

Donacia clavipes Fabricius
The preliminary stage and copulation act was observed in three and two pairs, respectively. During the preliminary stage the male placed segment 1 of the fore-tarsi on the anterior margin of the female's pronotum, and the remaining segments on her head between the eyes. His middle legs clasp the female's body behind the middle coxae. Male hind legs rest on the substratum behind the female elytral apex. During the copulation act the male places his fore-tarsi laterally on the female's pronotum with an inclination in front and down, or dorsally on the pronotum interior to the anterolateral calli, with the claws catching on the anterior margin of the pronotum. The position of the middle and hind legs of the male is similar to that during the preliminary stage.

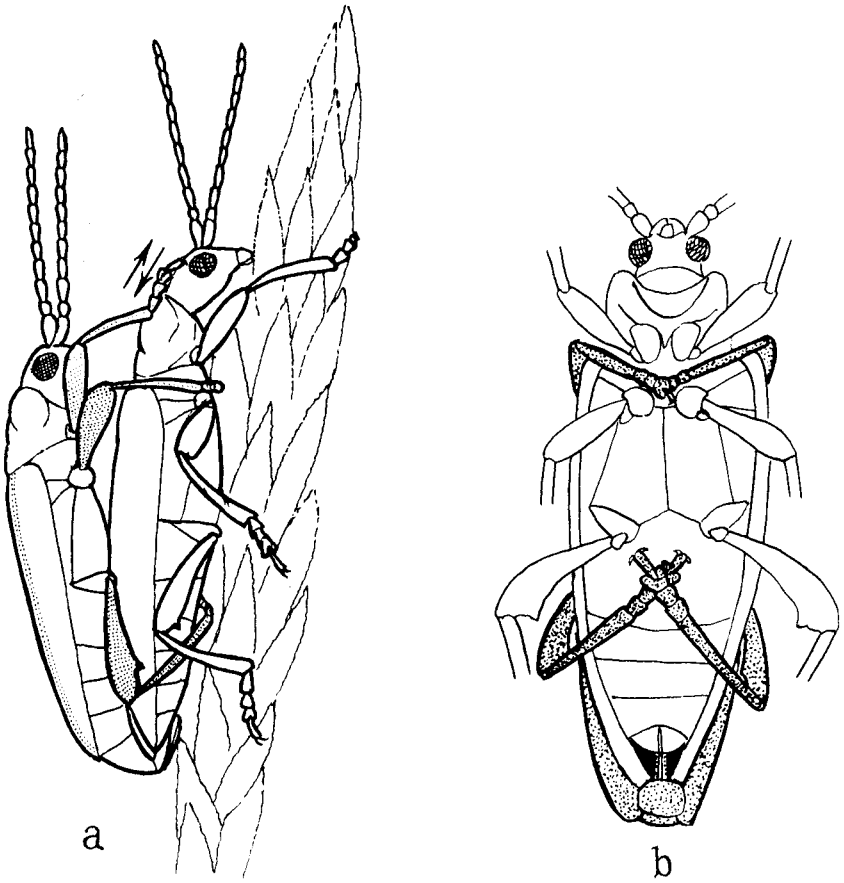

Fig. 1. Donacia brevitarsis: a) copulation on a stamen spike of *Carex vesicaria*, lateral view, b) position of middle and hind legs of male during copulation, ventral view. Arrows show the direction of male fore-tarsi rubbing.

Donacia crassipes Fabricius

In this species mating was observed in four pairs. The male performs the same courtship during the preliminary stage and copulation act. He puts his fore-tarsi on the female's vertex calli or on the pronotum interior to the anterolateral calli, or on the elytral base. The male rubs the female's vertex calli with his fore-tarsi now and then. His middle legs clasp the female body laterally, with his tarsi resting on her elytral epipleuri above the middle coxae, or on metasternum; his hind legs widely separated, with the tarsi placed on the substratum.

Donacia dentata Hoppe

The preliminary stage and copulation act were observed in four and one pair, respectively. During the preliminary stage the male puts his fore-tarsi on the female's head along the longitudinal axis with the segment 1 on the antennal calli, segments 2 and 3 on the antenna or between antennae. Sometimes the male places the segment 1 of one of his fore-tarsi on female's eye. The male rubs the female's antennal calli now and then. His middle legs clasp the female's humerae in front, with the tarsi meeting in front of her middle coxae and

directing backwards between them. The male's hind tibiae are brought together over the female's abdominal sternites, and the tarsi are directed backwards and placed on the substratum. During the preliminary stage the female is motionless or crawls. During the copulation act, the male places his fore-tarsi asymmetrically: the segment 1 of one tarsus on the female's antennal callus and that of the other tarsus on her eye. The position of the middle legs of the male is similar to that during the preliminary stage. His hind tarsi rest on the substratum when the female is motionless, and trail behind when she crawls.

Donacia marginata Hoppe
I failed to observe the mating behaviour of this species. Therefore, I cite a report by Medvedev & Pavlov (1987): "The male puts his fore-tarsi on the basal margin of the female's elytra, somewhat outside the pronotum", the middle legs "can settle on the female's hind femora in the central or apical part". The male "separates his antennae upwards and then brings them together in front of himself and touches the outside of the female's antennae".

Donacia obscura Gyllenhal
The preliminary stage and copulation act were observed in one and five pairs, respectively. During the preliminary stage the male places the fore-tarsi on the female head: the left tarsus between the antennal insertions, the other, right tarsus on the outside of the antennae. The male rubs the female head ever so slightly, but usually holds his fore-tarsi motionless. The male middle legs clasp the female humeri at the front, with the tarsi meeting on the mesosternite; his hind legs clasp her body, with the tarsi meeting on the abdominal sternite 2 and orientated almost perpendicularly to the longitudinal body axis. During the copulation act the male places his fore-tarsi in the following way: segments 1-3 on the female pronotum interior to the anterolateral calli, segment 4 on her head behind the vertex calli or eyes, or tarsi entirely on the female pronotum, or segments 1 and 2 on the pronotum and 3 and 4 on the head, and the claws on the vertex calli. The male rubs the female head now and then. His middle legs clasp the female body, with the claws catching in front or behind her middle coxae; the hind tibiae meet each other below her abdomen, and the tarsi are directed backwards and rest on the substratum or are directed forward and settle on abdominal sternites 1-3.

Donacia simplex Fabricius
The preliminary stage and copulation act were observed in three and one pair, respectively. During the preliminary stage the male places his fore tarsi on female's vertex calli or behind the eyes and weakly rubs her head now and then. His middle legs clasp her humeri in front or behind; the hind tarsi cross below her abdomen or catch on the elytral epipleuri. During the copulation act, segments 1 and 2 of the male's fore-tarsi rest on the female's pronotum interior to the anterolateral calli, segments 3 and 4 (or 4 only) are placed on her head. The male sometimes slowly rubs the female's head behind the eyes with the fore-tarsi. His middle legs clasp her body at the level of the metathorax, with the tarsi resting in front of, or immediately behind the hind coxae.

Donacia sparganii Ahrens
Mating was observed in two pairs. During the preliminary stage the male places his fore-tarsi on the female's head and rubs the vertex calli with segment 1. The male's middle legs

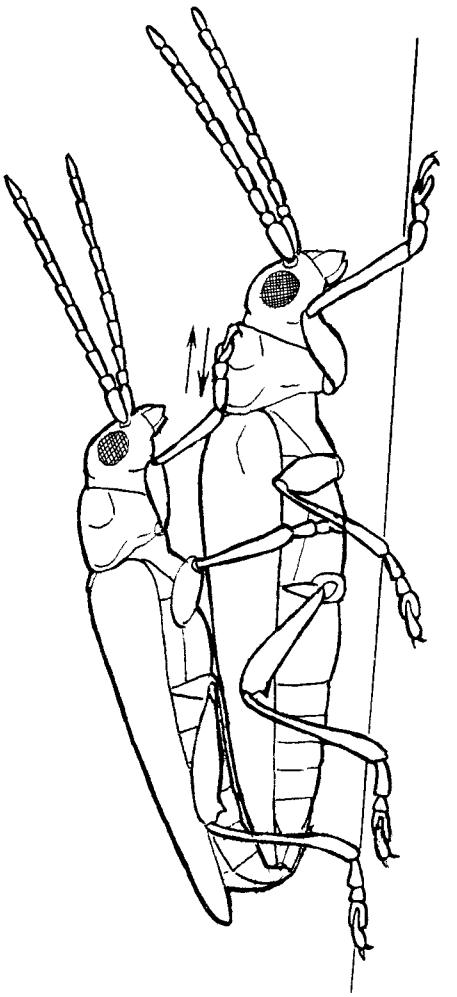

Fig. 2. Donacia thalassina. Copulation, lateral view. Arrows show the direction of male fore tarsi rubbing.

clasp the female's humeri in front or behind; his hind tarsi meet below her abdomen. During the copulation act the male puts segments 1 and 2 of the fore-tarsi along the midline of the female's pronotum, segments 3 and 4 on her head behind the eyes, or one tarsus between the antennae and the other between the antenna and eye. The male rubs the female's head and pronotum with the fore-tarsi and touches her antennae with his antennae in turn, as fast as he moves his fore-tarsi. The position of the male's middle and hind legs is the same as that of the preliminary stage, or the hind tarsi rest on the substratum.

Donacia thalassina Germar

Mating was observed in seven pairs. During the preliminary stage, the male rubs the female's vertex calli with segments 1 and 2 of the fore-tarsi, clasps her body between the fore and

middle or between the middle and hind coxae with his middle legs. The male's hind tarsi cross below the female's abdomen. During the copulation act the male places his fore-tarsi on the female's pronotum, or segments 2-4 on her head, behind the eyes and rubs them now and then. The position of the male's middle legs is similar to that during the preliminary period. The male's hind tarsi rest on the substratum when the female is motionless and trail, rarely cross below her abdomen, when she moves.

Donacia versicolorea (Brahm)
The preliminary stage and copulation act was observed in one and two pairs, respectively. The position of the male's fore and middle legs does not differ during the preliminary stage and the copulation act. The male puts his fore-tarsi on the female's pronotum interior to the anterolateral calli, with the claws catching on the anterior margin of the pronotum; his middle legs clasp her body between the middle and hind legs. The male's hind tarsi rest on the substratum during the preliminary stage, and trail freely during the copulation.

Donacia vulgaris Zschach
The preliminary stage did not occur in the three pairs observed. During the copulation act the male puts his fore-tarsi laterally on the female's pronotum with an inclination in front and down, or dorsally on the pronotum, interior to the anterolateral calli, or on the elytral base interior to the humeri. The male rubs the female's anterolateral calli now and then. His middle legs clasp the female's body laterally, with the tarsi positioned between her middle and hind coxae. The male hind tarsi rest on the substratum.

Plateumaris discolor (Panzer)
Mating was observed in one pair only. The male occupies the same position during the preliminary stage and copulation act. He puts his fore-tarsi laterally on the female's pronotum below the anterolateral calli with an inclination in front and down, and with the claws catching on the anterior margin of the proepimerae. The male's middle legs clasp the female's body between the middle and hind legs, the hind tarsi cross below her abdominal sternites.

Feeding during mating

At times, females of some species were observed to feed during the preliminary stage and copulation act. Namely, females of *D. bicolor* fed on leaves of *Sparganium erectum*, *D. versicolorea* – on leaves of *Potamogeton nutans*, *D. brevitarsis* – on spikes of *Carex vesicaria* and P. *discolor* – on spikes of *Eleocharis palustris*. Medvedev & Pavlov (1987) reported on the feeding during the mating, in females of *D. dentata* and *D. crassipes*.

Obviation danger during mating

In nature, the copulating pairs of *D. cinerea*, *D. thalassina*, *D. aquatica*, *D. brevitarsis*, *D. bicolor* and *D. crassipes* get unlinked and try to disappear independently (fall from the plant or fly upwards) as someone approaches. Olsoufieff (1913) and Medvedev & Pavlov (1987) noted that the beetles *D. dentata* and *D. malinovskyi* Ahrens, which copulate on floating leaves, crawl in water on the lower leaf surface and do not interrupt the mating in danger.

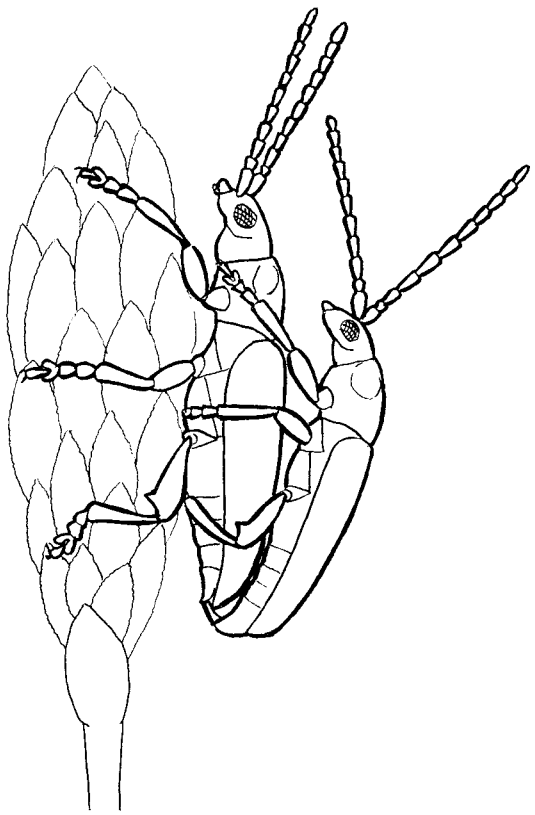

Fig. 3. Plateumaris discolor. Copulation on a spike of *Eleocharis palustris*, lateral view.

Completion of mating

From my observations the male usually leaves the female without the prior attempts by the female to drive him away at the end of mating. In one case, I observed a female of *D. sparganii* to push off a male with her right hind leg. In D. *aquatica* the female sometimes pushes her hind tarsi against the sides of the male's elytra and tries to pull off him backwards. Michelsen (1966) described a different manner by which a female releases herself from the male's embrace: "In *Donacia aquatica* the female is very restless after the end of copula and often performs "pendulum movements", i.e. the female stands upon the front and middle pair of legs, lifts her hind legs, and turns her body rapidly from side to side like a pendulum centred near the middle of the pronotum". Although I studied mating in this species, such interesting female behaviour was not noticed.

Conclusions

1. Mating behaviour was studied in 14 Palaearctic species of Donaciinae. It is subdivided into the following consecutive stages: 1) male takes the mating position, 2) preliminary

stage (+ precopulatory courtship), 3) copulation act (− copulatory courtship), and 4) end of mating.

2. One characteristic of mating in Donaciinae is the preliminary stage before the copulation act: the male occupies a certain position on the female's elytra and mostly performs a precopulatory courtship.

3. The copulatory courtship was found in 10 species.

4. Precopulatory and copulatory courtship consists of the rubbing of the female's antennal and vertex calli, the head behind the eyes, or the anterolateral calli of pronotum by the male's fore-tarsi. A courtship by the rubbing of the head is reported for the first time in the Coleoptera.

5. The well developed convex vertex calli are apparently present only in some species in which the courtship by rubbing of them occurs. They never occur in species in which the male does not touch the female's head.

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