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A behavioural inventory of adult *Stenus* species (Coleoptera: Staphylinidae)

OLIVER BETZ

Zoologisches Institut der Universität, Ökologie, Olshausenstr. 40,
D-24098 Kiel, Germany

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According to focal animal sampling, the genus-specific behaviour of *Stenus* beetles (Coleoptera, Staphylinidae) can be presented in the form of a comprehensive ethogram including 73 distinct behavioural patterns. Most observed behavioural patterns can be assigned to five functional systems: 'feeding', 'reproduction', 'grooming', 'resting' and 'protection'. In addition to grooming behaviour, searching behaviour takes a large amount of time (50–90% of the total observation time), which is indicative of the broad prey spectrum of *Stenus* species. The biological significance of selected behavioural aspects concerning 'searching for prey', 'prey capture', 'mating', 'self-grooming' and 'locomotion on the water surface' is addressed in the discussion.

KEYWORDS: Staphylinidae, *Stenus*, behaviour, behavioural inventory.

Introduction

The genus *Stenus* is composed of 1800 extant species (Central Europe: 120 species) that are distributed worldwide in damp environments (Puthz, 1971). This taxon is well defined by a modified elongated labium of the adults that can be rapidly protruded for prey capture (Schmitz, 1943; Weinreich, 1968; Betz, 1996). In order to investigate the adaptive value of their sophisticated labium, the predatory behaviour of *Stenus* species has been the subject of several recent studies (Bauer and Pfeiffer, 1991; Betz, 1998). These have shown that the specialized labial apparatus provides a biological advantage in that it permits relatively clumsy organisms (which appear to make up most of the recent *Stenus* species, with their limited reaction ability and agility) to catch prey items that are capable of rapid escape responses in a sudden and surprising manner.

Only a few references to single observations of the behaviour of *Stenus* species can be found in the literature (e.g. Billard and Bruyant, 1905; Benick, 1922; Delahon, 1926, 1927; Urban, 1928; Renkonen, 1934; Voris, 1934; Jenkins, 1960; Linsenmair, 1963; Lecoq, 1991) and no general survey of the genus-specific modes of behaviour is available so far. Therefore, the object of the present autethological study is to present a comprehensive ethogram, i.e. a list of all observable modes of behaviour

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that are shown by some adult Central European *Stenus* species that belong to various subgenera. This behavioural inventory is based on direct observations in terraria, video recordings and high speed cinematography and should provide a solid foundation for further quantitative behavioural or taxonomical studies of this genus.

Materials and methods

Focal-animal sampling

Several terraria (60 × 30 × 30 cm) were sparsely planted with grasses and sedges. In part, I covered the dark soil with moist plant detritus. The terraria were filled with water until the soil became saturated and small pools appeared on its surface. In order to test whether the beetles voluntarily crossed small bodies of water, I built an 8-cm-wide trench that crossed the terrarium 20 cm from its narrow edge. Along its margins, a rising shore was modelled and covered with fine sand. Into each terrarium, I put five specimens per species. Moreover, I provided the terraria with a number of potential prey organisms, e.g. springtails, aphids or small flies. In order to attain natural conditions, I situated the terraria outside. If required, they were protected from direct sunlight by a parasol. In order to avoid disturbance of the beetles, I observed each terrarium through the small openings of a screen. After a period of familiarization (24 h), I recorded all behavioural patterns that occurred for a focal animal during a sample period (60–90 min) continuously with the aid of a cassette tape recorder and a digital watch (e.g. Altmann, 1974; Colgan, 1978). Moreover, the length of time that a focal animal spent in different functional systems was noted. I recorded each species (other than *Stenus pubescens*, which was observed 11 times) twice in the morning, twice in the afternoon and twice in the early evening. Recordings were carried out between June and September. I followed the instructions of Colgan (1978) and Tembrock (1982, 1992) in preparing the ethogram. In all, I observed eight *Stenus* species that inhabit different biotopes (cf. Betz, 1998) in this manner: *S. bimaculatus* Gyllenhal, *S. canaliculatus* Gyllenhal, *S. comma* Leconte, *S. juno* (Paykull), *S. pubescens* Stephens, *S. similis* (Herbst), *S. solutus* Erichson and *S. flavipes* Stephens.

Film recordings

I used SVHS-video techniques and high speed cinematography in order to be able to analyse separately the predatory behaviour of *Stenus* species in detail. These recordings have previously been described in Betz (1998), in which the prey capture behaviour of 18 *Stenus* species is compared. Nevertheless, for the sake of completeness, all behavioural patterns that make up predation are included in a more concise form in the present ethogram.

In order to resolve the general locomotory behaviour on the water surface, I filmed the beetles in small glass cuvettes (2 × 2 × 2 cm) that were half filled with tap water. The bottom of these cuvettes was painted white, so that the menisci that were formed where the legs and body dimpled the water could be observed as shadows on the bottom (cf. Baudoin, 1976; Guthrie, 1989).

Video recordings were taken of 18 *Stenus* species, as listed in Betz (1998).

Results

The genus-specific behavioural inventory

In the following, the genus-specific behavioural inventory is given as a catalogue of all observed behavioural patterns. I assigned the modes of behaviour to the following functional systems: 'feeding', 'reproduction', 'grooming', 'resting' and 'protection'. In addititon, some patterns of behaviour (e.g. general modes of locomotion such as 'flying' or 'walking') could not be related to a specific functional system. These are categorized as 'other patterns'. Concerning the searching behaviour, it was not possible to determine whether it involved seeking prey, mates, places to rest or to lay eggs. Thus, I neutrally call this pattern 'searching'. However, in most cases, searching ended in predation and is, therefore, here assigned to the category 'feeding'. Each description of a behavioural pattern is followed by the names of the *Stenus* species in which it has been observed.

a. Functional system 'feeding':

a.1. Context 'searching':

a.1.1. 'Running with regular interruptions': fast forward movement in a stop and go pattern, i.e. alternating between running and stopping at regular short intervals (the runs last somewhat longer than the stops, which occur for approximately 1 s). Rhythmically moving the abdomen up and down during this pattern of locomotion: bending it upwards during the stops, bending it downwards at the beginning of the run and holding it horizontally during the run. Eventually circling the abdomen instead of moving it up and down during the stops (e.g. this is the usual behaviour of *S. biguttatus* (Linnaeus), *S. comma* and *S. fossulatus* Erichson). Often raising of head (and prothorax) during the jerky stops and turning towards the slightest motion in the surroundings. Turning also occurring spontaneously. Occasionally, superficial self-grooming during the stops.

Established in all investigated *Stenus* species.

a.1.2. 'Walking with regular interruptions': slow stepwise forward movement in a stop and go pattern, i.e. regularly alternating between walking and stopping (the walks being of shorter duration than the stops, which approximately last up to half a minute). Permanently reactively or spontaneously raising of the head (and prothorax) during the stops and turning towards the slightest motion in the surroundings. Occasionally, superficial self-grooming during the stops.

Established in all investigated *Stenus* species.

Graduations exist between patterns a.1.1. and a.1.2. Both patterns are shown both during climbing in the vegetation or in the plant debris and during walking on the flat ground surface.

a.1.3. 'Raising': reactive raising of the head (and prothorax) during patterns a.1.1. and a.1.2. (see above) or after longer periods remaining still in a specific position.

Established in all investigated *Stenus* species.

a.1.4. 'Turning': reactive turning of the head (and prothorax) towards the slightest motion in the surroundings even those occurring at distances of up to several centimetres. Shown during patterns a.1.1. or a.1.2. (see above) or after longer periods of remaining still in a specific position. Occasionally, performed immediately before moving directly to an adjacent reed.

Established in all investigated *Stenus* species.

a.1.5. 'Concurrent raising and turning': concurrent performance of patterns a.1.3. and a.1.4.

Established in all investigated *Stenus* species.

a.1.6. 'Inspecting potential food particles': using the mouthparts to inspect small particles (e.g. soil) that adhere to plants or debris. Occasionally picking them up with the mandibles and re-depositing them.

Established in *S. comma*, *S. juno*, *S. flavipes* and *S. pubescens*.

a.1.7. 'Attempting an ambush': remaining at a given place (up to 1 h), frequently swivelling up to 180° about its vertical axis (thus obtaining a view all around), turning immediately towards the slightest motion and possibly running towards it. Sometimes, running a few steps forward, raising the head (and prothorax) and, after a while, walking backward to the starting position.

Established in *S. comma* and *S. solutus*.

a.2. Context 'prey capture':

a.2.1. 'Running close': approaching the prey in a regular series of fast runs and stops until reaching the attack distance.

Established in all investigated *Stenus* species.

a.2.2. 'Pursuing': chasing the fleeing prey in a series of jerky fast runs, stops and alignments, each in response to the movements of the prey.

Established in all investigated *Stenus* species.

a.2.3. 'Stalking': warily approaching a scarcely moving prey step by step until reaching the attack distance. Occasionally, superficial self-grooming during the stops. Sometimes, walking a few steps backwards after finishing the approach.

Established in all investigated *Stenus* species.

a.2.4. 'Turning away': turning away from a prey that the beetle has previously approached. Preferentially shown when the prey is moving scarcely or not at all.

Established in all investigated *Stenus* species.

a.2.5. 'Seizing prey with the labium': orienting the longitudinal body axis until it is in alignment with the prey stimulus and, as soon as the critical attack distance is reached, stopping forward movement and then lunging forward while abruptly protruding the elongated labium (cf. figure 4 in Bauer and Pfeiffer, 1991 and figure 6 in Betz, 1998). During the strike, moving the antennae backward and moving the head in a prognathous position. After the strike, irrespective of capture success, retracting the labium within the reach of the mandibles. If necessary, accomplishing this with the help of the forward stretched fore legs. If the prey is immovable (e.g. plant-sucking aphids), drawing the body up to the prey by the adhering labium.

Established in all investigated *Stenus* species with the exception of *S. canaliculatus*.

While hunting in vegetation or in plant debris, the capture situations may differ from the pattern outlined so far: for example, it may be necessary to detach the foretarsi from the substratum and, additionally, to bend the prothorax (up to ~90°) against the abdomen in order to attain a favourable capture position and to reach prey that are otherwise out of range (figure 1). Such patterns were established in *S. cicindeloides* (Schaller), *S. similis*, *S. solutus* and *S. pubescens*.

Occasionally, the beetles attempted to strike minute particles of dirt that were situated on plants or on the pane of the terrarium and that were clearly contrasted against the background.

a.2.6. 'Seizing prey with the mandibles': orienting the longitudinal body axis until it is in alignment with the prey stimulus and, as soon as the critical attack distance is reached, stopping forward movement, opening the mandibles, lunging towards the prey and quickly grasping it with the mandibles. During the strike, moving the antennae backward and moving the head in a prognathous position.

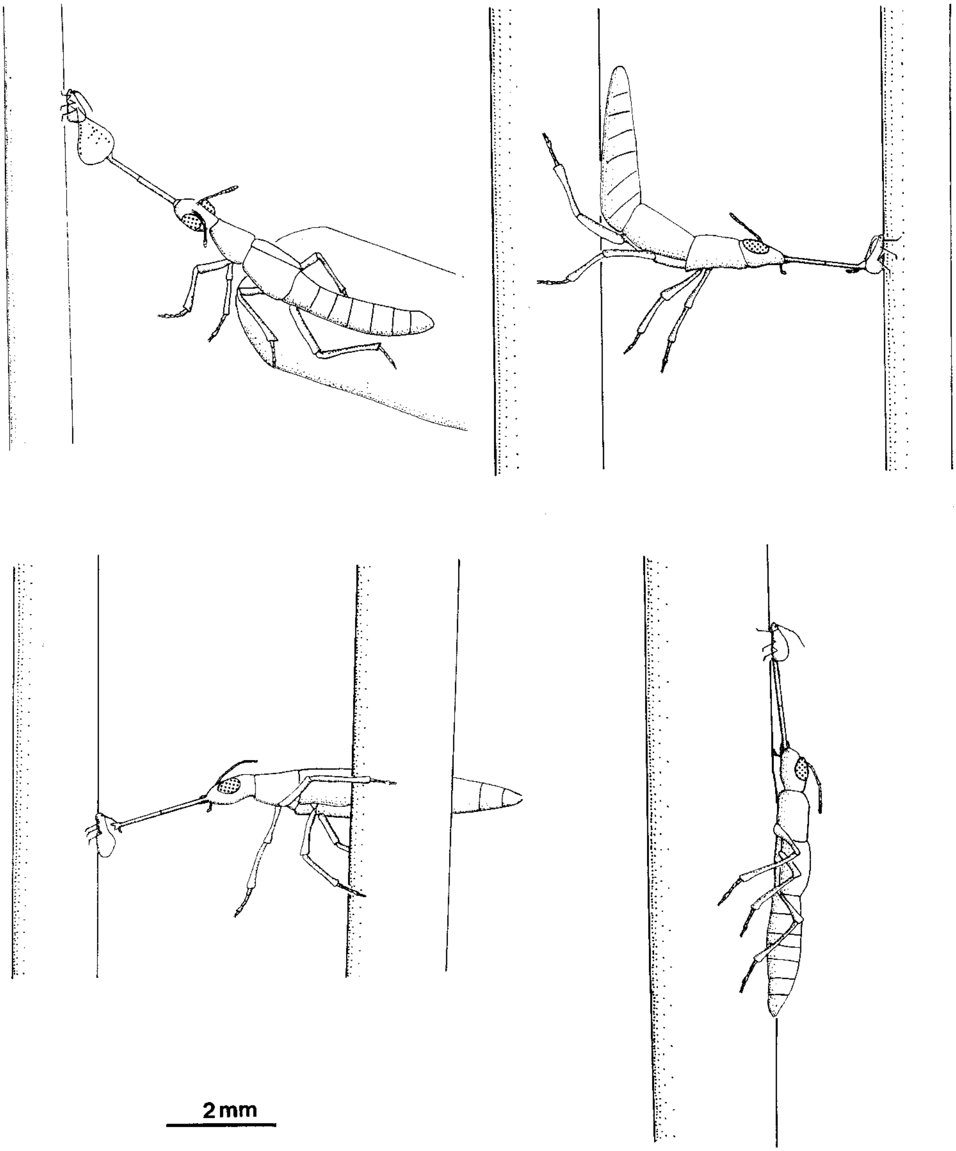

FIG. 1. *Stenus cicindeloides*. Characteristic capture situations occurring while hunting in vegetation or in plant debris.

After the strike, irrespective of capture success, moving the body backwards. Towards clumsy prey (e.g. aphids), the final strike may consist of simply picking up the prey with the mandibles without lunging towards it and attaining high capture velocities.

Established in all investigated *Stenus* species.

a.2.7. 'Mutually contending for seized prey': attempting to wrench a seized prey animal from a conspecific. Digging the mandibles into a prey that has been seized by a conspecific, resulting in a 'tug-of-war' for the prey. During this pattern, largely bending the abdomens upwards.

Established in *S. cicindeloides* and *S. pubescens*.

a.2.8. 'Depositing a seized prey animal': depositing a prey animal that has only just been seized and that is now incapable of escape. Occasionally, subsequent rubbing of the mandibles on the substratum.

Chiefly established towards aphids and gamasids in *S. comma*, *S. juno*, *S. pubescens*, *S. similis* and *S. solutus*.

a.2.9. 'Picking up a deposited prey animal': subsequent to pattern a.2.8, picking up the prey anew with the mandibles.

Established in *S. juno* and *S. solutus*.

a.2.10. 'Localizing a motionless prey animal by touch with the antennae': gently bringing together the stretched forward opened antennae subsequent to the approach (up to a critical attack distance) to a prey that suddenly has become motionless. At the slightest touch of the prey with the inner sides of the antennae performing pattern a.2.6 (figure 2).

Only established in *S. canaliculatus*.

a.2.11. 'Moving sideways along a motionless prey animal': slowly walking sideways along the longitudinal body axis of a relatively large prey animal (e.g. a last instar *Heteromurus nitidus* Templeton springtail) that has oriented its longitudinal body axis perpendicularly to that of the beetle and that has remained motionless following the approach of the beetle up to the critical attack distance. As soon as the edge of the prey is reached, performing pattern a.2.5. or a.2.6.

Established in *S. fossulatus* and *S. latifrons* Erichson.

a.2.12. 'Walking backwards with a seized prey animal': walking a few steps backwards with a prey animal held by means of the mandibles. Shown immediately subsequent to a successful seizure.

Established in all investigated *Stenus* species.

a.2.13. 'Walking forwards with a seized prey animal': walking forwards for a while with a prey animal held by means of the mandibles. Shown immediately subsequent to a successful seizure or to pattern a.2.12. Occasionally, during this pattern, raising of the prothorax in order to keep the prey away from the substratum.

Chiefly established towards relatively large prey animals (e.g. last instar *H. nitidus* springtails) in all investigated *Stenus* species.

a.2.14. 'Remaining still with a seized prey animal': remaining still for several seconds with a prey animal held by means of the mandibles, until the escape movements of the prey become weary. During this pattern, raising of the prothorax in order to keep the prey away from the substratum (figure 3). Shown immediately subsequent to a successful seizure or to pattern a.2.12.

Chiefly established towards relatively large prey animals in all investigated *Stenus* species.

a.3. Context 'food intake':

a.3.1. 'Feeding on the prey': kneading the pierced prey by rhythmically ab- and adducting the mandibles; this may entail (possibly with the help of the maxillae) rotatory movements of the prey. During this pattern, laterally spreading out the antennae and permanently vibrating the maxillae. Pushing brownish mid-gut juices out of the mouth and blending them with the prey material. After a while, gradually sucking in the prey material, which is now shapeless. Depending on the prey size, the whole procedure lasts up to several minutes. Feeding on the prey may be interrupted each time by new prey capture events, so that many small prey animals can be captured in succession.

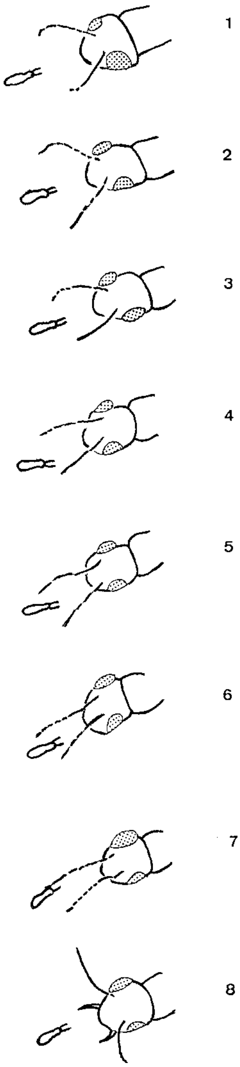

FIG. 2. *Stenus canaliculatus* beetle localizing a motionless springtail with its antennae. Time course of the depicted sequence [seconds that lapsed from the start (= picture 1)]: (1): 0.0; (2): 1.4; (3): 2.4; (4): 2.8; (5): 3.1; (6): 3.4; (7): 4.0; (8): 4.1.

Established in all investigated *Stenus* species.

a.3.2. 'Depositing and picking up food remains': depositing individual remnants of the prey and immediately picking them up again. Occurring during pattern a.3.1.

Established in *S. pubescens*.

a.3.3. 'Definite depositing of food remains': depositing of indigestible remains. Occasionally, scraping remains from the mouthparts with the fore legs. Occurring at the end of the food intake.

Established in *S. pubescens*.

a.3.4. 'Reinspecting food remains': repeatedly walking some steps away and returning to the place of ingestion in order to re-inspect food remains or to pick them up with the mandibles again. Occurring after the end of the food intake.

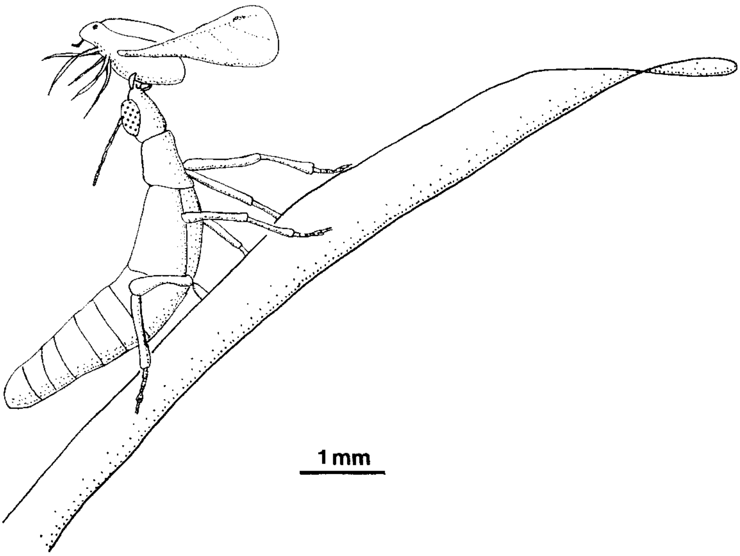

FIG. 3. *Stenus similis* beetle raising its prothorax in order to keep a captured aphid away from the substratum.

Established in *S. canaliculatus*, *S. juno* and *S. pubescens.*

a.3.5. 'Drinking': dipping of the mandibles in the moist substratum or small pools and taking in some fluid.

Established in all investigated *Stenus* species.

a.4. Context 'excretion':

a.4.1. 'Defecation': releasing a whitish droplet from the apex of the abdomen. This usually happens soon after food intake.

Established in all investigated *Stenus* species.

b. Functional system 'reproduction':

b.1. Context 'searching':

As mentioned above, it could not be determined whether searching behaviour was undertaken to find prey, mates or places to rest and to lay eggs. During searching behaviour, encounters with conspecifics usually resulted in attempts to copulate (provided that males were involved), whereas confrontations with potential prey animals led to prey capture. Therefore, no specific appetitive behaviour seems to exist for prey capture or reproduction (except pattern a.1.6). Consequently, the behavioural patterns a.1.1 to a.1.5 also seem to be valid for the search for mates.

b.2. Context 'mating':

In this context, I included the defence behaviour of specimens that are not ready to mate.

b.2.1. 'Turning': reactive turning of the head (prothorax and longitudinal body axis may follow) towards another individual.

Established in all investigated *Stenus* species.

b.2.2. 'Running close': male jerkily (with regular short interruptions) running close to another specimen.

Established in all investigated *Stenus* species.

b.2.3. 'Pursuing': chasing another specimen in a series of jerky fast runs, stops and alignments, each in response to the movements of the other specimen.

Established in all investigated *Stenus* species.

b.2.4. 'Remaining still while bending the abdomen upwards': two specimens facing each other at a distance of a few millimetres and remaining still while bending their abdomens upwards. Usually followed by an attempt to mate by one of the specimens.

Established in *S. canaliculatus*, *S. comma*, *S. juno*, *S. pubescens* and *S. solutus*.

b.2.5. 'Mounting': leaping up to a conspecific by a male, clinging to it and, while mounting parallel to it, trying to copulate.

Established in *S. canaliculatus*, *S. comma*, *S. flavipes*, *S. juno*, *S. pubescens* and *S. solutus*.

b.2.6. 'Mutual repeated touching of the abdomens': performing trembling movements of the (apices of the) abdomens by both mating partners, so that both abdomens frequently touch each other. Occurring immediately before or after copulation.

Established in *S. canaliculatus*.

b.2.7. 'Copulating in an end-to-end position': subsequent to pattern b.2.5 and after insertion of the aedeagus into the female genital orifice, the male turns it longitudinal body axis through 180° so that the mating partners are now oriented in opposite directions (end-to-end position), while being connected by the apices of their abdomens (figure 4a). Mating partners may remain in this position for up to one hour. During intromission, the female may remain still or, while moving around, drag the male behind her.

Established in *S. boops* Ljungh, *S. bifoveolatus* Gyllenhal, *S. canaliculatus*, *S. flavipes*, *S. fossulatus*, *S. pubescens* and *S. solutus*.

b.2.8. 'Copulating in a parallel position': throughout copulation, remaining in the parallel position taken up by the male during pattern b.2.5 (figure 4b). Mating partners may remain in this position up to several minutes.

Established in *S. comma*, *S. juno* and *S. providus* Erichson.

b.2.9. 'Running away from a conspecific': turning to a conspecific that has approached and subsequently running away from it.

It is not clear whether this pattern represents a general escape behaviour (belonging to the functional system 'protection') or whether it is a reaction of males

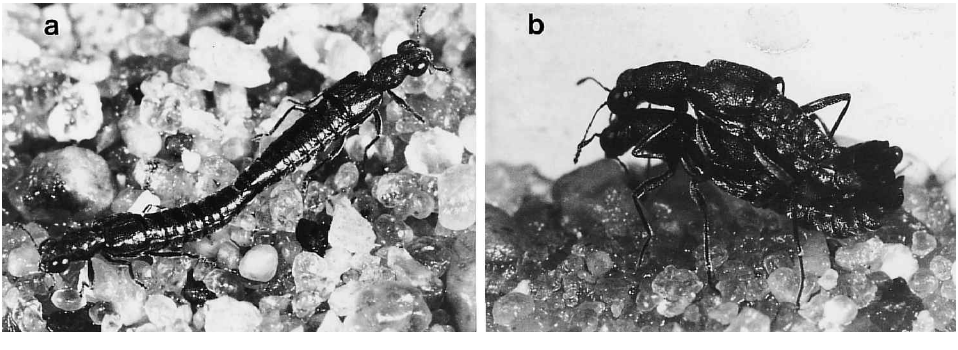

FIG. 4. Both copulation positions occurring in *Stenus* species: (a) *S. bifoveolatus* pair maintaining an end-to-end position; (b) *S. comma* pair in a parallel position.

or females being not ready to mate and is specifically released by the approach of a conspecific.

Established in *S. comma* and *S. pubescens*.

b.2.10. 'Yielding to a conspecific': yielding to a male willing to mate by walking backwards and bending the abdomen upwards.

Established in *S. juno*.

b.2.11. 'Shaking a conspecific off': hindering a mounted male in copulating by largely bending the abdomen upwards. Then, shaking it off by vehemently swinging the bent abdomen. This behaviour is shown both by females not ready to mate and by males mounted by mistake by another male.

Established in *S. canaliculatus*, *S. comma*, *S. flavipes*, *S. juno*, *S. pubescens* and *S. solutus*.

b.2.12. 'Separation after copulation': separating the linkage that has been formed by the mating partners for copulation. In species that copulate in the end-to end position (pattern b.2.7), the male turns its longitudinal body axis once again through 180° so that the mating partners are now oriented in parallel.

Established in *S. bifoveolatus*, *S. boops*, *S. canaliculatus*, *S. comma*, *S. flavipes*, *S. fossulatus*, *S. juno*, *S. providus*, *S. pubescens* and *S. solutus*.

b.2.13. 'Dabbing the apex of the abdomen': subsequent to pattern b.2.12, dabbing the apex of the abdomen on the substratum by the male and leaving a whitish droplet (probably seminal fluid).

Established in *S. comma*.

b.3. Context 'oviposition':

The deposition of eggs takes place in secrecy in minute gaps in the ground, beneath moist plant debris or within dead hollow stalks. Therefore, the egg-laying behaviour could not be directly observed. However, inspection of the boxes where the beetles were reared in the laboratory showed that some specimens produced dense egg clusters consisting of up to 20 eggs (established in *S. bimaculatus*, *S. comma* and *S. juno*). In contrast, other specimens tended to lay eggs in smaller looser clutches or even separately (established in *S. bifoveolatus*, *S. cicindeloides*, *S. pubescens* and *S. solutus*).

c. Functional system 'grooming':

In connection with the food intake, grooming behaviour took place not only subsequent to, but also during feeding on the prey (pattern a.3.1). Otherwise, grooming behaviour occurred independently of the food intake. While doing so, the specimens usually remained at a specific location and did not move around. Sometimes, superficial self-grooming occurred during the locomotion pauses (cf. patterns a.1.1 and a.1.2). In most cases, grooming behaviour started with rubbing the hind tarsi against the apex of the abdomen and, while doing so, taking a secretion from the pygidial gland and gradually spreading it with the middle and fore legs on the body surface.

In detail, the following patterns, which are classed under the general term 'self-grooming', could be distinguished:

'Self-grooming':

c.1. Rubbing the fore legs against the head, mouthparts and the antennae. Primarily occurring after food intake. According to video recordings of

S. bimaculatus, *S. canaliculatus* and *S. juno*, also pulling the tibia and the tarsus through the opened mandibles.

Established in all investigated *Stenus* species.

c.2. Rubbing of the mandibles on the substratum after food intake.

Established in *S. bimaculatus*, *S. canaliculatus* and *S. comma*.

c.3. Bending the apex of the abdomen downwards by curving the middle abdominal segments upwards. While doing so, bending the apex of the abdomen aside and rubbing the hind legs (tarsi) against it.

Established in all investigated *Stenus* species, except *S. canaliculatus*.

c.4. Rubbing the hind legs (especially tarsi and tibiae) against each other.

Established in all investigated *Stenus* species.

c.5. Rubbing a hind leg against a middle leg.

Established in all investigated *Stenus* species.

c.6. Rubbing a middle leg against a fore leg.

Established in all investigated *Stenus* species.

c.7. Simultaneously rubbing both middle legs against both fore legs.

Established in *S. latifrons*.

c.8. Rubbing both fore legs against each other.

Established in *S. juno*.

c.9. Rubbing one or both hind legs against the upper, lateral or underside of the abdomen.

Established in all investigated *Stenus* species.

c.10. Rubbing one hind leg against the lateral side of the abdomen and, simultaneously, rubbing the contralateral middle leg against the fore leg.

Established in *S. canaliculatus*.

c.11. Rubbing a hind leg against the apex, the upper or the lateral side of the abdomen and, sinultaneously, rubbing the contralateral hind leg against a middle leg.

Established in *S. canaliculatus* and *S. pubescens*.

c.12. Rubbing one hind leg against the abdomen and, simultaneously, rubbing one or both fore legs against the head, the mouthparts or the antennae.

Established in *S. canaliculatus*, *S. juno* and *S. pubescens*.

c.13. Rubbing one hind leg against the lateral side of the abdomen and, simultaneously, rubbing the contralateral middle leg against the underside of the thorax.

Established in *S. juno*.

c.14. Opening the elytra, spreading the hindwings and vigorously rubbing the apex and the upper side of the abdomen against them. Spreading of the hind wings may or may not be managed with the help of the (posterior margins of the caudal tergites of the) abdomen (in many *Stenus* species, cuticular edges or close-set setae situated at the posterior margins of the tergites 7–10 serve as morphological devices for this purpose (Puthz, 1971)).

Established in *S. bimaculatus*, *S. canaliculatus*, *S. comma*, *S. pubescens* and *S. similis*.

c.15. Folding the hind wings beneath the elytra with the help of the upwardly bent abdomen.

Established in *S. bimaculatus*, *S. canaliculatus*, *S. comma*, *S. pubescens* and *S. similis*.

c.16. Bending the abdomen forward and rubbing its apex against the upper side of the elytra.

Established in *S. solutus*.

c.17. Rubbing both fore legs (tarsi) against the protruded labium (figure 5). While doing so, frequently protruding and retracting the labium.

Established in *S. bimaculatus*, *S. comma*, *S. geniculatus* Gravenhost, *S. juno*, *S. pubescens*, *S. similis* and *S. solutus*.

d. Functional system 'resting':

During resting behaviour, the beetles remain almost motionless for a while (up to 90 min or even longer) at a specific location (usually in vegetation or debris) and appear to be less reactive to movements in their surroundings. This behaviour may be interrupted for only a moment in order to change the resting position. I considered all such behavioural patterns to be resting periods when they lasted longer than 1 min.

In detail, the following patterns could be distinguished:

'Sitting':

d.1. Sitting on a horizontal or vertical structure (e.g. a leaf sheath). The head may be adjusted downwards or upwards at a vertical structure.

Established in all investigated *Stenus* species.

d.2. Sitting on a vertical structure, while adjusting the longitudinal body axis perpendicularly to it.

Established in *S. similis*.

d.3. 'Changing the resting position': turning the body axis (frequently at 180°) and (or) moving a few steps forwards. Then resting again. Occurring subsequent to patterns d.1 and d.2.

Established in all investigated *Stenus* species.

d.4. 'Ending of resting': rhythmically moving the abdomen up and down.

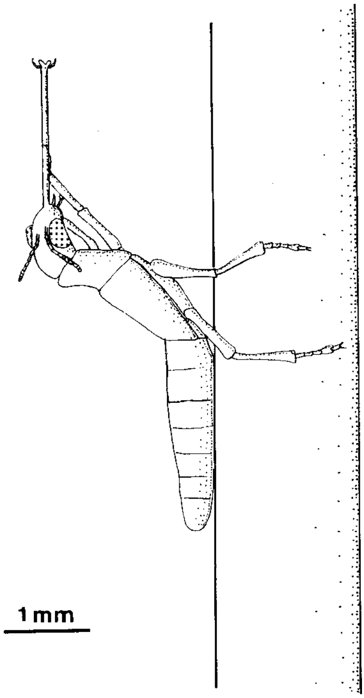

FIG. 5. *Stenus cicindeloides* beetle grooming its protruded labium.

Occurring just before becoming active after a period of resting (e.g. in order to walk around or to change the resting position).

Established in all investigated *Stenus* species.

d.5. 'Sitting, while continuously moving the abdomen': sitting for a while at a specific location and, while doing so, slowly circling the abdomen or moving it up and down. The abdominal movement may cease so that the beetles remain motionless for some time, with the abdomen being bent upwards and the body being raised.

It is not clear whether this behaviour represents a true resting pattern. It may be associated with other behavioural systems, such as reproduction or thermoregulation.

Established in *S. flavipes*, *S. juno*, *S. pubescens*, *S. similis* and *S. solutus*.

e. Functional system 'protection':

e.1. 'Yielding and running away': yielding to another relatively large arthropod (e.g. a bug) that is approaching. Frequently, beforehand, turning towards and eventually going even nearer to the approaching individual as in patterns a.1.4 and a.2.3. However, in contrast, these patterns are not followed by prey capture but by taking to flight (running away). During escape, running in a continuous manner differing from the jerky locomotion pattern a.1.1.

Established in *S. comma*, *S. flavipes* and *S. pubescens*.

e.2. 'Akinesis': feigning death for several seconds (sometimes while lying on its back). Occurring subsequent to strong shakings of the substratum or grasping the beetles with forceps.

Established in *S. boops*, *S. canaliculatus*, *S. cicindeloides*, *S. fossulatus*, *S. impressus*, *S. juno*, *S. latifrons*, *S. providus*, *S. similis* and *S. solutus*.

e.3. 'Chemical defence': the following observations have been established in calculated confrontations with *Formica rufa* Linné ants.

Subsequent to being grasped by an ant, the beetle is immediately released. Therefore, it seems to be completely invulnerable to such attacks. Occasionally, it slightly bends the apex of the abdomen towards the body (head) of the grasping ant, resulting in immediate release and the confused running around of the attacker. However, the repellent effect of the defensive secretion does not seem to depend on its directed application by the apex of the abdomen but appears to emanate from the entire body surface of the beetles.

Established in *S. bifoveolatus*, *S. cicindeloides*, *S. comma*, *S. juno*, *S. latifrons*, *S. nitidiusculus* Stephens, *S. pubescens* and *S. solutus*.

f. 'Other patterns':

f.1. 'Travelling directly between adjacent plant structures': in order to move directly to an adjacent plant structure (e.g. a stalk). This involved jackknifing the prothorax, detaching the fore and middle legs one after another from the substratum and, once the fore and middle tarsi have come into contact with the adjacent stalk, detaching the hind legs, so that the rest of the body can follow. It occurs while the beetles are climbing in dense vegetation or plant debris.

Established in all investigated *Stenus* species.

f.2. 'Walking on the water surface': walking on the water surface as if it were firm ground, while being supported by the surface tension (and sometimes by material such as dust and debris deposited on the water surface). Occasionally, while doing so, the apex of the abdomen is bent downwards by curving the middle abdominal segments upwards so that it comes in contact with the water surface and, in addition to the legs, supports the body against the water surface. During this type of locomotion, only the tarsi and the apex of the abdomen have contact with the water surface.

Predominantly occurring when the beetles voluntarily cross small bodies of water.

Established in *S. boops*, *S. cicindeloides*, *S. comma*, *S. juno*, *S. pubescens* and *S. solutus*.

f.3. 'Swimming on the water surface': while being supported by the surface tension, swimming on the water surface and attaining velocities of 2–3 cm/s; rowing with all three pairs of legs following the common rhythm of terrestrial insect walking (e.g. Hughes and Mill, 1974). This forward movement is supported by swinging the abdomen to and fro (figure 6), while the head oscillates from side to side. During this type of locomotion, the tarsi, tibiae and the entire undersurface of the body make contact with the water surface. The forward (not backward) thrust lasts up to twice as long as in terrestrial locomotion. The stroke motions represent movements typical of swimming in aquatic beetles (cf. figures 7 and 13 in Nachtigall, 1974):

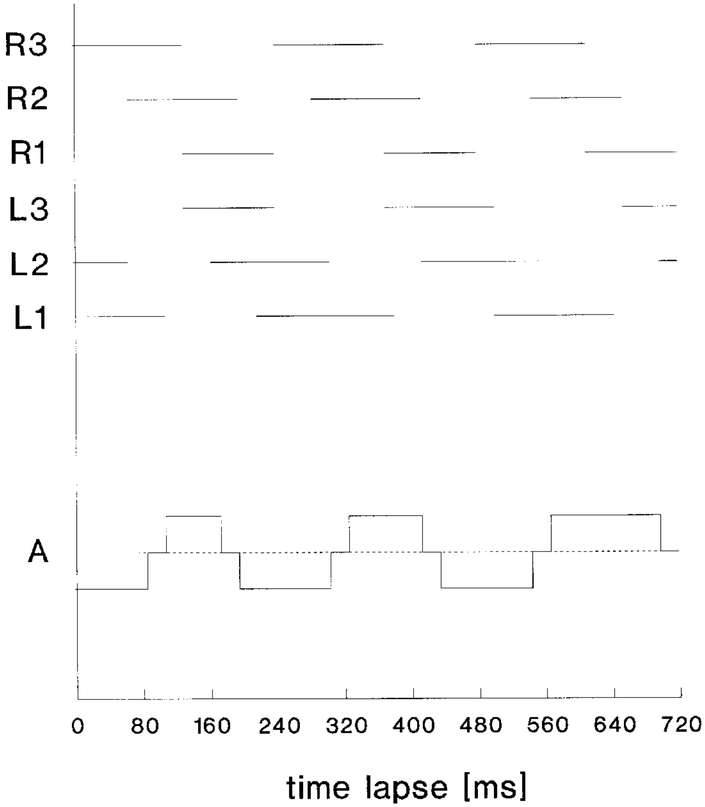

FIG. 6. Movement pattern of the legs and the abdomen of a swimming *Stenus cicindeloides* beetle. The horizontal axis represents time. The solid bars indicate protraction. The rectangular wave form represents the swinging of the abdomen to and fro and its deviation from the longitudinal body axis, which is symbolized by the dashed line. Abbreviations: R = legs on the right body side, L = legs on the left body side, A = abdomen.

during the power stroke the extended leg is retracted and the water surface is indented by the tarsi. During recovery of the leg, the femur swings forward, while the tibia is flexed upon it and, at the anterior turning point, the tibia and tarsus are swung outwards. The tarsi indent the water surface only a little or are even lifted from the water surface.

Established in *S. bimaculatus*, *S. bifoveolatus*, *S. boops*, *S. cicindeloides*, *S. clavicornis* (Scopuli), *S. comma*, *S. fossulatus*, *S. juno*, *S. latifrons*, *S. nitidiusculus*, *S. pubescens*, *S. solutus* and *S. tarsalis* Ljung.

f.4. 'Skimming the water surface': rapidly skimming the water surface by releasing a spreading-active abdominal secretion (cf. Jenkins, 1960) and thus attaining velocities of 45–70 cm/s (cf. Linsenmair, 1963; Nachtigall, 1974). While skimming, setting the middle and hind legs against the body and steering by movements of the abdomen. Occurring in combination with pattern f.3 or when unintentionally falling down on to the water surface. Moreover, skimming is probably sometimes undertaken in order to overcome the attractive force of the meniscus during pattern f.6.

Established in *S. bimaculatus*, *S. cicindeloides*, *S. comma*, *S. fossulatus*, *S. latifrons*, *S. nitidiusculus*, *S. pubescens* and *S. tarsalis*.

f.5. 'Flying': opening the elytra, spreading the hind wings and non-directively flying away. The beetles are reluctant flyers and, therefore, flying usually taking place in the terraria when an attempt is being made to escape adverse temperatures (~ 30°C) temporarily occurring at noon in the summer.

Established in *S. canaliculatus*, *S. comma* and *S. pubescens*.

f.6. 'Leaving a stalk in order to move on to the water surface': in order to leave a stalk and to move on to the water surface, walking, head first, to the base of the stalk, detaching the fore and middle legs one by one from the substratum and, once the fore and middle tarsi have come into contact with the water surface, detaching the hind legs, so that the rest of the body can follow. The beetle can then skim down the plant and the adjacent meniscus on to the water surface (figure 7). While doing so, it bends its abdomen forward (probably, in order to avoid being wetted). However, it sometimes adheres to the meniscus on account of the capillary attractant forces and, therefore, does not detach itself from the plant straight away. In this case, it becomes separated from the stalk by rapid swimming movements (pattern f.3) and is eventually supported by releasing the spreading-active agent (cf. pattern f.4).

Established in *S. cicindeloides*, *S. pubescens* and *S. solutus*.

f.7. 'Slicing the pupal cocoon': the hatched adult slices the pupal cocoon with the mandibles in order to leave it.

Established in *S. pubescens*.

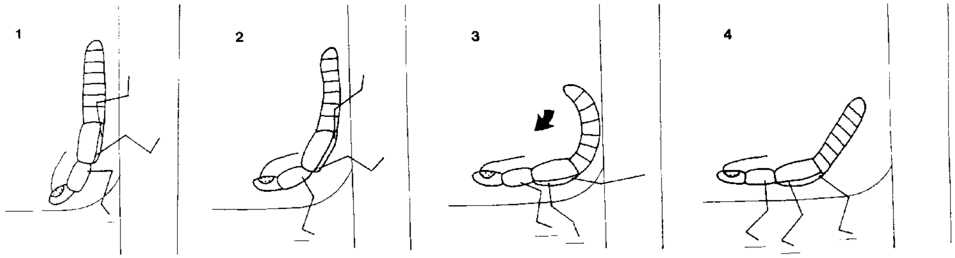

FIG. 7. Stenus pubescens beetle leaving a stalk in order to move on to the water surface. The arrow indicates the skimming movement down the meniscus.

Time budgets

Activities without a specific duration (e.g. prey capture events) influence the time budgets of the specimens to a negligible extent. Therefore, the functional systems 'food intake' and 'reproduction' are mainly recruited from the durations of 'searching' (including 'feeding on the prey') and 'copulation', respectively. For the reasons mentioned above, the neutral term 'searching' is preferred to the term 'food intake' in the following diagrams. These diagrams give general hints to the time that is spent by the beetles in different functional systems (results exemplified for four species in figure 8). Most specimens spent large amounts of time (50–90% of the total observation period) searching (for prey). Grooming behaviour occurred in nearly all investigated individuals and amounted to 50% of the observation period. However, in most cases, it made up 5–30%. In *S. canaliculatus*, *S. comma* and *S. juno*, resting behaviour had the same order of magnitude, whereas in *S. flavipes*, *S. pubescens*, *S. similis* and *S. solutus*, it amounted to a longer part of the observation period. In five of the six investigated specimens of *S. similis*, it constituted by far the major part.

The duration of reproduction behaviour varied from specimen to specimen, of course, because it depended on whether a copulation was achieved during an observation period.

Discussion

To date, thorough descriptions of the behaviour of staphylinid beetles are infrequent in the literature and concern only single observations or specific behaviour systems (e.g. Voris, 1934; Strassen, 1957; Lipkow, 1966, 1968; Peschke, 1978; Blum, 1979; Jepson, 1984; Forsyth and Alcock, 1990). This is also true for the genus *Stenus*, which has received increased attention on account of its apomorphic labial apparatus (Schmitz, 1943; Weinreich, 1968; Bauer and Pfeiffer, 1991; Betz, 1996, 1998) and its skimming capability (e.g. Jenkins, 1960; Linsenmair, 1963). In order to provide a more general idea of the genus-specific behavioural patterns, this investigation presents a so-called first-order ethogram (cf. Tembrock, 1992) for the adults. It is hoped to be complete, since 19 species from five of the six current subgenera have been studied (seven species representing four subgenera have been thoroughly observed by focal-animal sampling) and no new behavioural patterns have been recognized during the course of the observations. However, specific life forms represented by myrmecophilous and arboricolous species (Puthz, 1971) have not been investigated so far and may exhibit further behavioural patterns. Moreover, specific patterns concerning aggregation in winter quarters (e.g. in tussocks) could not be directly observed. In addition, Lecoq (1991) describes gregarious behaviour in *S. cordatus* Gravenhorst that probably serves to overcome adverse droughts.

Most of the observed modes of behaviour can be assigned to five functional systems. The biological significance of selected behavioural patterns will be discussed in the following, according to this classification.

Functional system 'feeding'

Searching for prey. Throughout, searching behaviour that usually leads to prey capture takes a large amount of time (figure 8). This is in accordance with the remarks of Curio (1976) that, depending on the prey density, searching by predators in the field may amount up to 80% of the total time available. From this point of view, it becomes clear that these beetles have to be polyphagous, since, according

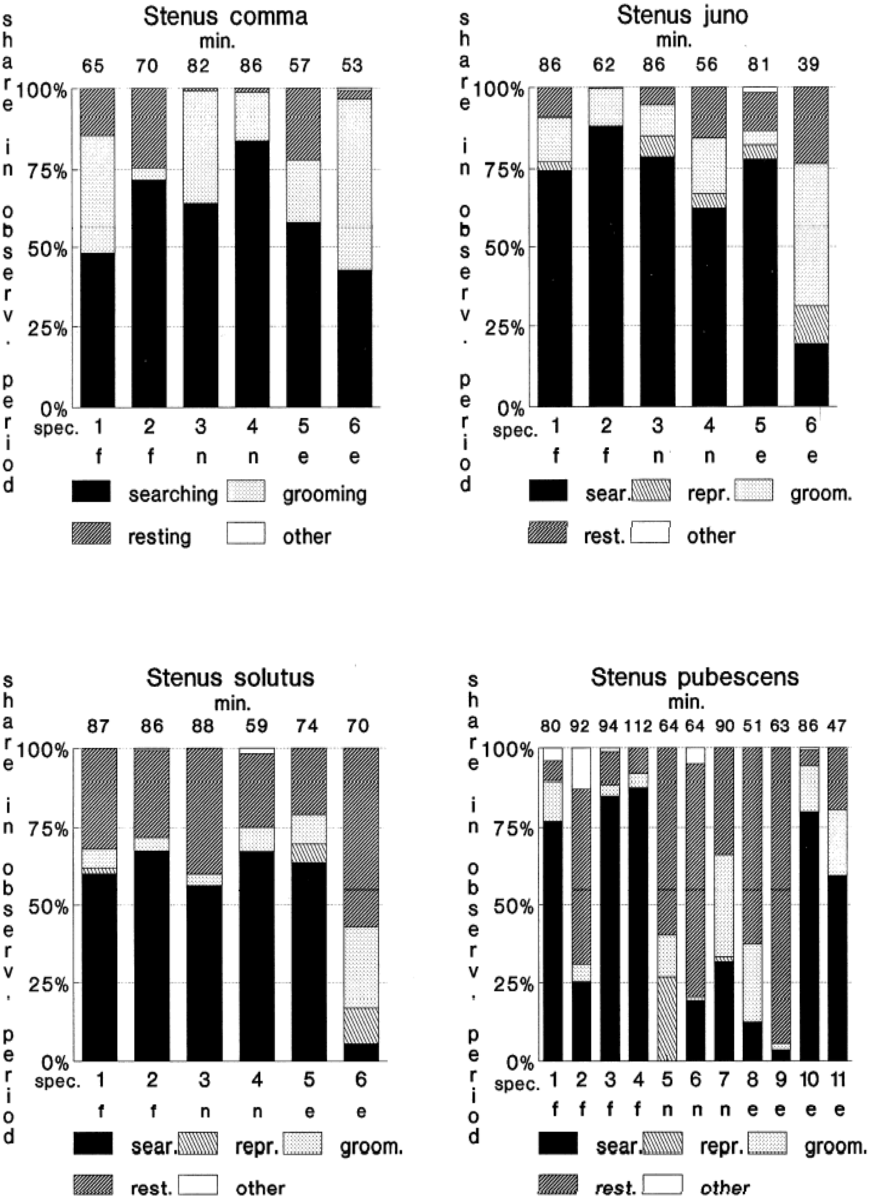

FIG. 8. Duration of time spent in different functional systems exemplified for four *Stenus* species.The results are given separately for each specimen. The total amount of time of observation (minutes) is given above the bars. Abbreviations: min. = minutes, spec. = specimen, f = forenoon, n = (after)noon, e = evening, sear. = searching, repr. = reproduction, groom. = grooming, rest. = resting, other = other patterns.

to theory, predators with long searching and short handling times ought to be generalistic feeders (cf. Begon *et al.*, 1991). Indeed, beetles have been observed to have a broad prey spectrum (Betz, 1998).

Searching is primarily visually guided but may be complemented by chemical cues. This seems likely, because the beetles, while moving around, permanently move their maxillary palpi to and fro, for instance. However, turning to and pursuing moving prey is solely visually guided. While searching, the beetles do not move continuously, but with regular interruptions in a stop and go manner (patterns a.1.1 and a.1.2). This type of locomotion is thought to be especially useful in visual hunters, since it may prevent noisy signals and help to discriminate between stationary and moving objects ('saltatory search' according to O'Brien *et al.*, 1989; Bell, 1990). Scanning for potential prey is probably only performed during the regular locomotion pauses, since the beetles only then reactively raise or turn towards movements in their surroundings.

The function of the peculiar stereotyped movements of the abdomen during normal walking (patterns a.1.1 and a.1.2) is subject to speculation. These movements may serve to support ventilation or they may signal relative immunity to predators.

In addition to the minute search of the structures of the habitat (which is in the usual searching mode in *Stenus* beetles), another type termed 'attempting an ambush' (pattern a.1.7) has been observed in *S. comma* and *S. solutus*. The supposed adaptive values of both searching modes have been discussed in Betz (1998).

Prey capture. Important aspects of prey capture behaviour have been thoroughly discussed in Bauer and Pfeiffer (1991) and Betz (1998), where it has been demonstrated that the specimens of most *Stenus* species probably rely on their rapidly protrusible labium that allows them, in spite of their limited agility and reaction ability, to capture prey capable of rapid escape responses. Only the individuals of a few species that are adequately agile and quick to react have refined the mandible-attack-mechanism.

Interestingly, the specimens of some species which hunt in the vegetation even respond to stationary particles contrasting against the background. This might occur because the beetles create relative image motions by their own movements (cf. Wehner, 1981). In this context, pattern a.2.11 ('moving sideways along a motionless prey animal') may also serve to visualize prey that tends to freeze during the approach of the beetles and that therefore is no longer stimulating. At the same time, motion parallax may be used as an additional cue (cf. Wehner, 1981). A behavioural pattern that is analogous to pattern a.2.11 has been observed in jumping spiders (Forster, 1977).

An alternative behaviour that serves to localize motionless prey is shown by the specimens of *S. canaliculatus*, which find prey by means of their antennae (figure 2). A similar pattern is known in *Coenagrion* larvae (Odonata, Coenagrionidae) (Alverdes, 1924).

As mentioned in Betz (1998), in mandible attacks, the beetles are capable of combining the final forward lunge with a taxis component (torsion of the head on the longitudinal axis of the body) in order to adjust to the form, direction of movement and location of the prey. Comparable taxes are performed by *Aeschna* larvae (Odonata, Aeschnidae) during their strike with the labium (Buchholtz, 1970). Adjusting movements such as these are classed with 'open-loop' responses, i.e. form, location and orientation of the prey are determined for the final time immediately before the strike.

Functional system 'reproduction'

As in other investigated staphylinid species from different genera (e.g. *Aleochara* Gravenhorst: Peschke, 1978; *Philonthus* Curtis: Jepson, 1984; *Tachinus* Gravenhorst and *Tachyporus* Gravenhorst: Lipkow, 1966 and *Velleius* (Fabricius): Strassen, 1957), the *Stenus* male is the more active partner in the courtship. A prolonged pre-copulatory phase is not established and the male rapidly attempts to mount the female and tries to copulate. However, this may be forestalled by a non-receptive female by means of several antagonistic behavioural patterns (cf. patterns b.2.9–b.2.11). It is not known whether receptive females produce chemical attractants and to what extent possible chemical cues (e.g. surface pheromones) are responsible for sex or species identification.

Interestingly, two different copulation positions can be observed in *Stenus* species (figure 4): whereas specimens of most investigated species hold an end-to-end position (cf. pattern b.2.7), the individuals of some species of the subgenus *Stenus* s. str. copulate in the parallel position (pattern b.2.8). However, even within this subgenus, both mating positions co-exist, since *S. fossulatus* specimens perform the usual end-to-end position. Both positions appear to be associated with different durations of insemination; copulation in the parallel position never lasts longer than several minutes, whereas mating in the end-to-end position may take up to one hour.

Functional system 'grooming'

Self-grooming makes up an important part of the behavioural inventory of adult *Stenus* species, since it is performed not only subsequent to feeding, but also occurs regularly in context with other functional systems. It amounts to a substantial part of the total time budget and consists of a large variety of distinct movement patterns (cf. patterns c.1–c.17). The main object of this extensive self-grooming appears to be to spread a pygidial secretion over the entire body surface. While doing so, the beetles sometimes make use of the considerable motility of their abdomen, since they are able to bend it forwards until its apex comes in contact with the upper side of the elytra (cf. pattern c.16). Apart from the spreading agent stenusin, Schildknecht *et al.* (1976) and Kanehisa and Tsumuki (1996) have shown that mixed pygidial secretions act as antimicrobics, fungicides and irritant defensive secretions. Therefore, frequently impregnating the body surface with the pygidial secretion may serve to prevent infestation with bacteria or fungi. In addition, the observed interactions with ants suggest that these grooming activities make the beetles unpalatable to other predatory arthropods.

Moreover, self-grooming may serve to spread a wax-like secretion from specific dermal glands all over the body surface in order to maintain water repellency.

Self-grooming is usually shown in an ample manner. In contrast, superficial self-grooming consisting of cursory rubbing movements of the legs occasionally takes place while searching for prey (cf. patterns a.1.1 and a.1.2) or stalking it. Most probably, this pattern is not real self-grooming but represents a displacement activity, as shown by *Aeschna* larvae (Odonata, Aeschnidae) while searching for prey (Hoppenheit, 1964).

Locomotion on the water surface

The beetles are capable of moving on the water surface in three different ways: walking, swimming or skimming. A comparison of walking with swimming shows that both types of locomotion follow the same mode of leg co-ordination characteristic of terrestrial insect walking (e.g. Wilson, 1966; Hughes and Mill, 1974). However, both modes of locomotion differ with respect to the stroke motions of the single legs, since the beetles perform characteristic swimming movements while being on the water surface. Such motions have also been established in some water beetles (cf. Hughes, 1958; Nachtigall, 1974; Gewecke, 1985) and water bugs (cf. Wendler *et al*., 1985) and serve to maximize the propulsive forces (Nachtigall, 1974). Certainly, the propulsive forces generated during the stroke do not appear to be much greater than the forces of drag during recovery, since the beetles often do not move ahead when performing swimming movements. However, the swinging movements of the abdomen and the intermittent release of the spreading agent may compensate for this deficiency.

Conclusion

The task of this study has been to present a survey of the genus-specific behaviour of adult *Stenus* species as a base for future ecological, behavioural or taxonomical studies on this genus. Certainly, interspecific differences may exist in the expression and frequency of the specific behavioural patterns that can be interpreted according to the ecology of the various species. Concerning predation, such differences have been investigated in Betz (1996, 1998). Moreover, some rare behavioural patterns (a.1.7, a.2.10, a.2.11 and b.2.8) appear to be restricted to relatively few *Stenus* species and, therefore, may be of taxonomic value.

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References

ALTMANN, J., 1974, Observational study of behaviour: sampling methods, *Behaviour*, **49**, 227–267.

ALVERDES, F., 1924, Beobachtungen an Ephemeriden- und Libellenlarven, *Biologisches Zentralblatt*, **43**(6), 577–605.

BAUDOIN, R., 1976, Les insectes vivant a la surface et au sein des eaux, in P.-P. Grassé (ed.) *Traité de Zoologie*, Tome VIII, Fasc. IV (Paris: Masson), pp. 843–926.

BAUER, T. and PFEIFFER, M., 1991, 'Shooting' springtails with a sticky rod: The flexible hunting behaviour of *Stenus comma* and the counterstrategies of its prey (Coleoptera, Staphylinidae), *Animal Behaviour*, **41**, 819–828.

BEGON, M., HARPER, J. L. and TOWNSEND, C. R., 1991, *Ökologie* (Basel: Birkhäuser), 1024 pp.

BELL, W. J., 1990, Searching behavior patterns of insects, *Annual Review of Entomology*, **35**, 447–467.

BENICK, L., 1922, Paarungsvorgang bei *Stenus*-Arten, *Entomologische Blätter*, **18**, 94.

BETZ, O., 1996, Function and evolution of the adhesion-capture apparatus of *Stenus* species (Coleoptera, Staphylinidae), *Zoomorphology*, **116**, 15–34.

BETZ, O., 1998, Comparative studies on the predatory behaviour of *Stenus* spp. (Coleoptera, Staphylinidae): the significance of its specialized labial apparatus, *Journal of Zoology, London*, **244**, 527–544.

BILLARD, G. and BRUYANT, G., 1905, Sur un mode particulier de locomotion de certains *Stenus*, *Comptes Rendus des séances de la Société de Biologie et des filiales*, 102–103.

BLUM, P., 1979, Zur Phylogenie und ökologischen Bedeutung der Elytrenreduktion und Abdomenbeweglichkeit der Staphylinidae (Coleoptera). Vergleichend- und funktionsmorphologische Untersuchungen, *Zoologisches Jahrbuch für Anatomie*, **102**, 533–582.

BUCHHOLTZ, C., 1970, Der Beutefang der Larve von *Aeschna cyanea*, *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 362–364.

COLGAN, P. W., 1978, *Quantitative Ethology* (New York: John Wiley & Sons), 364 pp.

CURIO, E., 1976, *The Ethology of Predation* (Berlin: Springer), 250 pp.

DELAHON, P., 1926, Kleine Mitteilung, *Entomologische Blätter*, **22**(3), 140.

DELAHON, P., 1927, Kleine Mitteilung, *Entomologische Blätter*, **23**(2), 90.

Forster, L. M., 1977, A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae), *New Zealand Journal of Zoology*, **4**, 51–62.

Forsyth, A. and Alcock, J., 1990, Ambushing and prey-luring as alternative foraging tactics of the fly-catching rove beetle *Leistotrophus versicolor* (Coleoptera: Staphylinidae), *Journal of Insect Behaviour*, **3**(6), 703–718.

Gewecke, M., 1985, Swimming behaviour of the water beetle *Dytiscus marginalis* L. (Coleoptera, Dytiscidae), in M. Gewecke and G. Wendler (eds) *Insect Locomotion* (Berlin: Parey), pp. 111–120.

Guthrie, M., 1989, Animals on the surface film, in *Naturalists' Handbook* (Slough: Richmond Publishing Co.), **12**.

Hoppenheit, M., 1964, Beobachtungen zum Beutefangverhalten der Larven von Aeschna cyanea Müll. (Odonata), *Zoologischer Anzeiger*, **172**, 216–232.

Hughes, G.M., 1958, The co-ordination of insect movements. III. Swimming in *Dytiscus*, *Hydrophilus* and a dragonfly nymph, *Journal of Experimental Biology*, **35**(3), 567–583.

Hughes, G. M. and Mill, P. J., 1974, Locomotion: terrestrial, in M. Rockstein (ed.), *Physiology of Insecta*, Vol. III (New York: Academic Press), pp. 335–379.

Jenkins, M. F, 1960, On the method by which *Stenus* and *Dianous* (Coleoptera: Staphylinidae) return to the banks of a pool, *Transactions of the Royal Entomological Society London*, **112**, 1–14.

Jepson, S. B., 1984, Mating behaviour in two closely related sympatric species of *Philonthus* (Coleoptera: Staphylinidae), *Journal of Natural History*, **18**, 411–423.

Kanehisa, K. and Tsumuki, H., 1996, Pygidial secretion of *Stenus* rove beetles (Coleoptera: Staphylinidae), *Bulletin of the Research Institute for Bioresources Okayama University*, **4**(1), 25–31.

Lecoq, J.-C., 1991, Observation d'un comportement rare chez un staphylin: le grégarisme (Col. Staphylinidae), *L'Entomologiste*, **47**(3), 173–174.

Linsenmair, K. E., 1963, Eine bislang unbekannte Fortbewegungsart bei Insekten: Das Entspannungsschwimmen, *Kosmos*, 331–334.

Lipkow, E., 1966, Biologisch-ökologische Untersuchungen über *Tachyporus*-Arten und *Tachinus rufipes* (Col., Staphylinidae), *Pedobiologia*, **6**, 140–177.

Lipkow, E., 1968, Zum Eiablage-Verhalten der Staphyliniden, *Pedobiologia*, **8**, 208–213.

Nachtigall, W., 1974, Locomotion: mechanics and hydrodynamics of swimming in aquatic insects, in M. Rockstein (ed.) *Physiology of Insecta*, Vol. III (New York: Academic Press), pp. 381–432.

O'brien, W. J., Evans, B. I. and Browman, I., 1989, Flexible search tactics and efficient foraging in saltatory searching animals, *Oecologia*, **80**, 100–110.

Peschke, K., 1978, Funktionsmorphologische Untersuchungen zur Kopulation von *Aleochara curtula* Goeze (Coleoptera, Staphylinidae), *Zoomorphologie*, **89**, 157–184.

Puthz, V., 1971, Revision der afrikanischen Steninenfauna und Allgemeines über die Gattung *Stenus* Latreille (Coleoptera, Staphylinidae), *Annales de Musée Royal de L'Afrique Centrale*, *Serie in-8°*, **187**, 1–376.

Renkonen, O., 1934, Über das Vorkommen der *Stenus*-Arten (Col. Staph.) an verschiedenen Wohnorten in Finnland, *Annales Zoologici Societatis Zoologicae Botanicae Fennicae Vanamo*, **1**(4), 1–33.

Schildknecht, H., Berger, D., Krauss, D., Connert, J., Gehlhaus, J. and Essenbreis, H., 1976, Defense chemistry of *Stenus comma* (Coleoptera: Staphylinidae) LXI., *Journal of Chemical Ecology*, **2**(1), 1–11.

Schmitz, G., 1943, Le labium et les structures bucco-pharyngiennes du genre *Stenus* Latreille, *Cellule*, **49**, 291–334.

Strassen, R. Zur, 1957, Zur Ökologie des *Velleius dilatatus* Fabricius, eines als Raumgast bei *Vespa crabro* Linnaeus lebenden Staphyliniden (Ins. Col.), *Zeitschrift für Morphologie und Ökologie der Tiere*, **46**, 243–292.

Tembrock, G., 1982, *Spezielle Verhaltensbiologie*, Band I, (Stuttgart: Fischer), 528 pp.

Tembrock, G., 1992, *Verhaltensbiologie* (Jena: Fischer), 385 pp.

Urban, C., 1928, Stenus auf dem Wasser laufend, *Entomologische Blätter*, **24**, 45.

Voris, R., 1934, Biologic investigations on the Staphylinidae (Coleoptera), *Transactions of the Academy of Science of Saint Louis*, **28**(8), 232–261.

Wehner, R., 1981, Spatial vision in insects, in H. Autrum (ed.) *Comparative Physiology and*

Evolution of Vision in Invertebrates, Handbook of Sensory Physiology, **7**(6c) (Berlin: Springer), pp. 287–616.

Weinreich, E., 1968, Über den Klebfangapparat der Imagines von *Stenus* Latr. (Coleopt., Staphylinidae) mit einem Beitrag zur Kenntnis der Jugendstadien dieser Gattung, *Zeitschrift für Morphologie und Ökologie der Tiere*, **62**, 162–210.

Wendler, G., Teuber, H. and Jander, J. P., 1985, Walking, swimming and intermediate locomotion in *Nepa rubra*, in M. Gewecke and G. Wendler (eds) *Insect Locomotion* (Berlin: Parey), pp. 103–110.

Wilson, D. M., 1966, Insect walking, *Annual Review of Entomology*, **11**, 103–122.