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The behaviour and ecology of *Bembecinus hungaricus* FRIVALDSKY, 1876 (Hymenoptera: Apoidea: Sphecidae) in Austria

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Zusammenfassung

Verhalten und Ökologie von *Bembecinus hungaricus* FRIVALDSKY, 1876 (Hymenoptera: Apoidea, Sphecidae) in Österreich.

Eine dichte Nestaggregation von *Bembecinus hungaricus* FRIVALDSKY, 1876 wurde auf Flugsanddünen in Drösing, Niederösterreich, untersucht. Nahezu alle Verhaltensweisen dieser Art stimmen mit denen anderer Vertreter der Gattung überein. Die Wespen waren bei Temperaturen von 25 °C bis 45 °C aktiv. Die Tiere zeigten während des gesamten Tages hohe Aktivität und besondere Aktivitätsmuster konnten beobachtet werden: Die Nester wurden nur in den Morgenstunden kontrolliert, wogegen Beutetiere während des gesamten Tages eingetragen wurden. Die Weibchen verbringen die Nacht und Schlechtwetterperioden in Schlafnestern mit kurzen Gängen. Die Lufttemperatur in den Kolonien schwankte stärker als die Bodentemperatur in der Tiefe des Nestes. Die Larven wurden progressiv mit Zikaden, vorwiegend aus der Familie Cicadellidae, versorgt. Die Männchen schlüpften vor den Weibchen und verschwanden innerhalb der ersten fünf Wochen der Saison gänzlich von den Kolonien. Die Nester wurden von drei Fliegenarten, *Senotainia albifrons*, *Metopia* cf. *campestris*, *Paragusia elegantula* (Sarcophagidae, Miltogramminae) parasitiert. *Bembecinus hungaricus* zeigte eine Nistplatz-Präferenz für sandige Areale ohne Vegetation.

Abstract

A population of *Bembecinus hungaricus* FRIVALDSKY, 1876 was observed nesting in dense aggregations on sand dunes in Drösing, Lower Austria. Most behavioural traits of this species conform with other members of the genus. The wasps were active at air temperatures of 25 °C to 45 °C. Activity was high during all daylight hours and certain activity patterns were observed: nests were cleaned and inspected only in the morning whereas provisioning continued throughout the day. Female *B. hungaricus* spent the night and cold weather periods in short oblique sleeping burrows. Air temperature at the colony showed higher amplitudes than the temperature at the depth of the breeding cell. The larvae were progressively provisioned with leafhoppers, predominantly of the family Cicadellidae. Males emerged earlier than females and disappeared within the first 5 weeks of the nesting season. Nests were parasitized by the three miltogrammine flies *Senotainia albifrons, Metopia* cf. *campestris,* and *Paragusia elegantula* (Sarcophagidae, Miltogramminae). *Bembecinus hungaricus* showed a preference for sandy areas without vegetation.

Keywords: *Bembecinus hungaricus,* Sphecidae, activity patterns, habitat preference, Lower Austria.

Introduction

The genus *Bembecinus* A. COSTA, 1859 is the second largest in the subfamily Bembicinae (sesu MENKE 1997) and consists of 170 species. It's members occur on

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all continents and on many islands (BOHART & MENKE 1976). The behaviour and ecology of many species is well described (EVANS 1955, EVANS AND O`NEILL 1986, EVANS et al. 1986, LÜPS 1969, 1973). Morphological characteristics of *B. hungaricus* in Japan were published by TSUNEKI (1965, 1971). Only SCHMIDT & WESTRICH (1983) provided data on the biology of this species, specifically on its food plant. The main distribution area of *B. hungaricus* is southern Europe, but it also occurs in warmer parts of Central Europe (DE BEAUMONT 1954, SCHMID-EGGER & NIEHUIS 1997). The presented study deals with activity patterns, male behaviour, and habitat selection of *B. hungaricus,* as observed in 1998 and 1999 at sand dunes in Drösing, northeastern Austria. At that location *B. hungaricus* nested in the highest densities ever reported for this species. Microclimatic measurements supported the investigations of favoured habitats. Detailed data about nesting behaviour and prey species will be described in an accompanying paper (Zolda, in prep.).

Material and Methods

Study site

The study was conducted in Drösing, Lower Austria, near the Slovakian border, during the summers of 1998 and 1999. The study area is called "In den Sandbergen" and mainly consists of sand dunes in the middle of a pine forest (*Pinus sylvestris*). As elsewhere in Lower Austria, these dunes are of postglacial age. The former mobility of the dunes diminished with the growth of plants upon them and their expansion

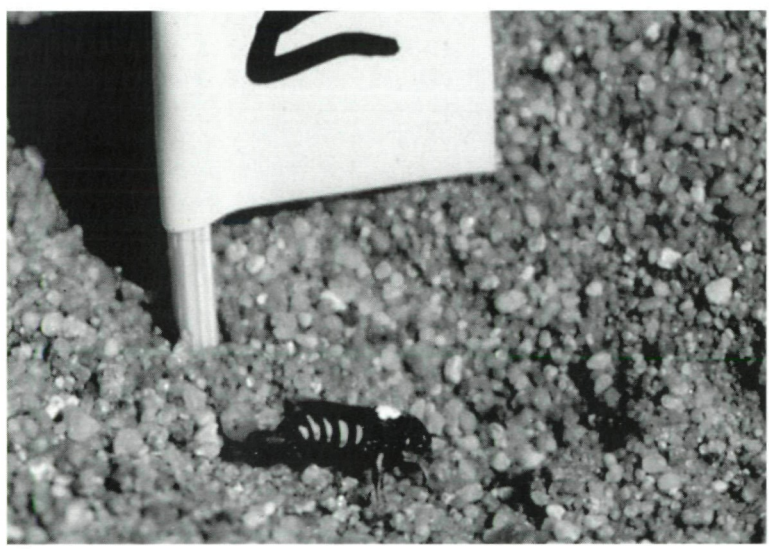

Fig. 1: Marked female of *B. hungaricus*, Dösing, Lower Austria.

was reduced through permanent afforestation during the last centuries. Despite the plant growth on the dunes, many plots of bare and friable sand have remained. This part of Austria is strongly influenced by the Pannonian climate with its warm and dry summers. The *Thymo angustifolii-Corynephoretum* plant association, which grows on the moderately to highly acidic soil (WIESBAUER & MAZZUCCO 1997), covers most of the area. *B. hungaricus* nested in high densities at plots of bare sand within this 20 ha site. The study site includes four colonies: a 5 m² bare sandy road, which is frequently used by cars or motorbikes (site A); 3 m² on a sandy road with sparse vegetation beneath a pine forest (site B); a 10 m² plot of bare sand in the middle of the *Thymo angustifolii-Corynephoretum* plant association (site C); a 150 m² sand pit surrounded by young trees of *Robinia pseudoacacia*, *Populus nigra* and *Salix* sp.(site D). The term colony is used in the sense of a preferred site for nesting with higher densities. OLBERG (1959) termed this type of sphecid aggregation a pseudocolony. The sandpit was bulldozed in autumn 1998 and many *B. hungaricus* nests were destroyed.

Observation period

Bembecinus hungaricus was observed from 29 June until 14 July 1998 only at sites B and C. Thereafter, no specimen was found and none of the marked specimens of these sites was detected again at any site in 1998. Research was continued at site A and D from 15 July until 23 August 1998. In 1999 the species was frequently observed at site D and sporadically at site A. The vegetation cover of sites B and C, assessed with a vegetation stratimeter Vstrat 901, increased from 20 % of the surface in 1998 to 50 % in 1999. After the bulldozing the surface of site D consisted of coarse-grained sand in 1999.

A total of 45 female wasps were marked for individual identification with different coloured dots of flashy enamel paint (Sakura paint marker) on the thorax dorsum. Recapturing the wasps for identification each time they returned to the nests was therefore unnecessary. They were captured with a small hand-net, either when they started to dig out the nest entrances or when they just exited their burrow. Neither the paint nor the net disrupted the wasps' behaviour: they showed no cleaning behaviour or unusual activity after capture and marking. The nest entrance of each marked female was marked with toothpicks (see Fig 1). Activity patterns of the marked females were observed on 16 days for a minimum of 5 hours per day starting at 9.00.

Abiotic factors (see Tab. 1)

Microclimatic conditions – air temperature (Ta) and relative humidity (RH) - of the nesting sites were measured during the nesting season 15 cm above the ground with a shaded datalogger Testostor (XL 175). The temperature in the depth of the breeding cell (Tc) was determined in both years during 14 days in July and August, the estimated developmental phase of *B. hungaricus,* with a second datalogger which was

	Air temperature (°C)		Soil temperature (°C)		Relative humidity (%)	
	1998	1999	1998	1999	1998	1999
Range	4.4 - 41.8	3.1 - 39.8	15.8 - 40.5	18.0 - 35.8	14.4 - 99.9	18.7 - 99.9
Mean ±SD	21.6 ± 7.8	20.4 ± 7.8	26.7 ± 5.8	23.4 ± 4.1	67 ± 25.3	70.2 ± 24.9

Tab. 1: Air temperature, soil temperature and relative humidity at the colony of *B. hungaricus* in two years of observation.

buried in the sand in a depth of 8 cm. Both sensors recorded the data at one hour-intervals. The temperature of the soil surface (Ts) and relative humidity under insolation were determined by placing a sensor in the middle of the colony when activity of *B. hungaricus* started.

Parasites

Parasitic flies were identified by Prof. Dr. Wolfgang Waitzbauer, University of Vienna, and Peter Sehnal, Natural History Museum Vienna.

Results

Temperature and Humidity

Ts was monitored on 13 days for the entire daily activity period and varied from 30 °C to 56 °C. Typically it reached its maximum between 13:00 and 14:00. In the morning hours, when the wasps started provisioning, Ts usually exceeded 25 °C and during midday the values climbed to 44 °C. During full insolation RH ranged from 9% to 46% the high values being associated with low air temperatures. A typical profile (19 July 1999) of in Ta, Ts, Tc and RH is shown in Fig. 2.

Values (range, mean ± SD) of Ta, Tc and RH recorded with the dataloggers in 1998 and 1999 are summarised in Table 1. Daily mean values of Ta ranged from 14.9 °C to 29.4 °C (1998) and from 15.2 °C to 26.3 °C (1999). Air temperature differed significantly between 1998 and 1999 ($t = 2.7$; $df = 96$; $p < 1.0$). The daily mean values of Tc varied from 21.5 °C to 30.8 °C in 1998 and from 17.8 °C to 25.8 °C in 1999. According to Ta, Tc differed significantly between the two years ($t = 8.84$; $df = 58$; $p < 0.01$). The variation of daily mean temperatures was higher for Ta than for Tc. Temperatures in the soil had lower amplitudes compared to air temperature. Accordingly Tc-mean values can exceed those for Ta (Fig. 3).

Activity (see Fig. 4)

Bembecinus hungaricus emerged in mid-June and females were active until mid-

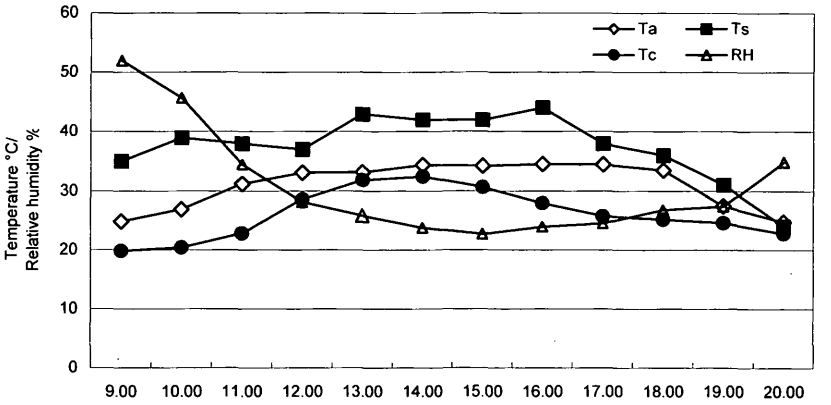

Fig 2: Typical daily profile (19. 7. 1999) of air temperature (Ta), surface temperature (Ts), soil temperature in cell depth (Tc) and relative humidity (RH) at the nesting area of *B. hungaricus* in Drösing.

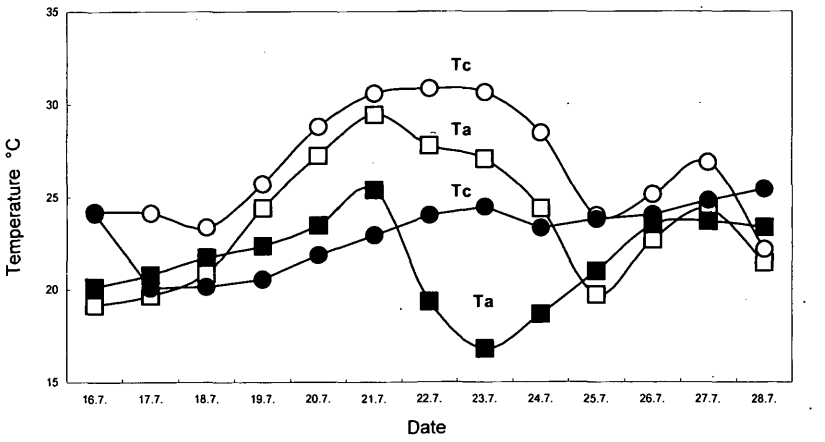

Fig. 3: Daily mean values of soil temperature in 8 cm depth (TC) and air temperature (Ta) of a two week period in 1998 (white symbols) and 1999 (black symbols).

September. The activity peaked in August. Females nested in high densities up to 21 nests per m² on bare sand measuring only a few square meters. Distances between nests were often less than 5 cm, and females disrupted one another during digging, provisioning and orientation flights. The majority of the population, consisting of hundreds of females, nested at site D.

Activity in the colony usually started between 9.00 and 10.00 and was high throughout the day. The females followed certain activity patterns, which are shown in

Fig. 4. In the morning they usually inspected the nest before they started provisioning which continued throughout the day.
The females flew 5 cm to 30 cm high above the surface in the hovering typical of the genus. As temperatures increased, flight frequency and flight speed also increased. Even during midday, when the surface temperatures reached 50 °C, *B. hungaricus* remained active. While searching for nests they kept their wings flat on the dorsum and tapped the antennal tips on the surface. *Bembecinus hungaricus* showed highest activity above 30 °C and in sunny weather. Under cloudy conditions females stopped provisioning and digging and appeared to warm up themselves on the warm sand by depressing their bodies to the surface and absorbing heat by conduction from the sand. In general, activity decreased when temperatures fell below 25 °C. After one week of hot days, when the weather was muggy,. and immediately prior to summer thunder storms, no specimen was seen at the colonies. In contrast, *Ammophila terminata*, *Harpactus elegans*, *Bembix rostrata*, *Bembecinus tridens* and *Oxybelus* sp., which nested at the edge of the colony, remained active under these conditions. In the morning or the late afternoon, females visited flowers of *Fallopea convolvulus*, *Polygonum aviculare* or *Erigeron* sp. The wasps were also sitting on plants, cleaning their abdomen with the hindlegs or pulling their antennae through the cleaning nick of the forelegs.

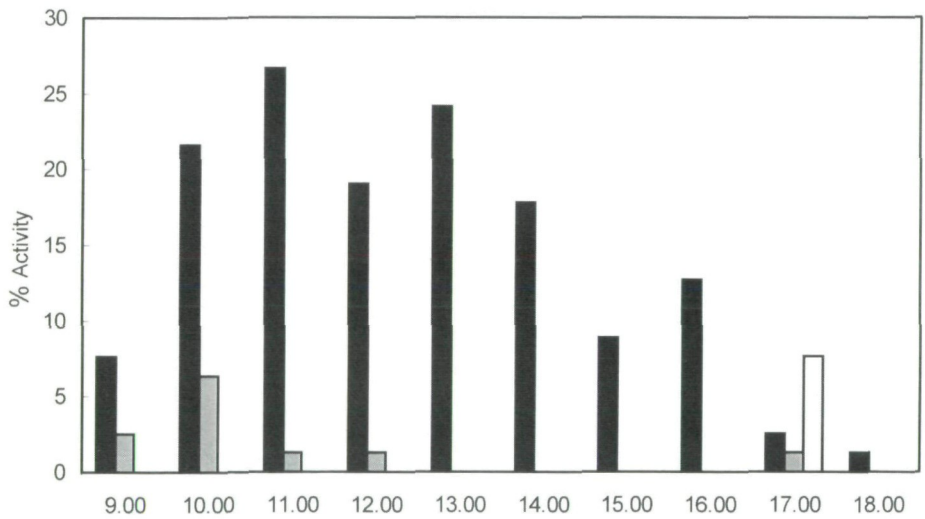

Fig. 4: Patterns of the daily activity in *B. hungaricus* based on observations of 45 marked female wasps. Values on the x-axis refer to the intervals beginning at the sketched time (9:00 describes the interval 9:00 to 9:59). Black columns refer to provisoning activity, grey columns to inspection, white columns to records of digging sleeping nests.

Between 17:00 and 18:00, when they had completed the daily provisioning, females started to dig their sleeping burrows (Fig. 4). This process lasted 8 min to 22 min (mean = 15.4 min; N = 7). A sleeping nest consisted of an oblique burrow with a slight expansion at the terminal end. The burrows were about 5 cm long and the wasps closed them from inside with a plug of soil. The wasps remained there on rainy or cold days. The first sign of activity in the morning was the removal of the sand from the entrance. The opened sleeping burrows were abandoned and new ones were dug each afternoon. After a few days the soil was perforated with holes, which were either opened sleeping burrows or resulted from unfinished digging activity. The integrity of the surface was quickly reconstituted by rainfalls.

Provisioning

Before starting provisioning, females inspected or cleaned the nests by throwing sand out of the burrows. Nests were sealed temporarily by scraping the sand in front of the nest over the entrance each time the wasps left. They thus levelled the mound of sand which they had previously piled up. Under suitable weather conditions female provisioning behaviour began between 9:00 and 10:00 (earliest record 9:35), continued through the day and finished between 17:00 and 18:00 (latest record 18:00) (Fig. 4). Provisioning wasps were skittish on the ground and flew away at the slightest provocation. They spent only a short time in the nest between provisioning trips. Provisioning never took longer than 3 min (N = 104) and typically less than 30 s. The wasps were disorientated when the soil surface had been disturbed by footprints, when another female dug close by, or when parasitic flies posed a threat. The females then flew in circles above the nesting area until they found their entrance. The intervals between two consecutive provisionings varied from 11 min to 3 h 58 min (mean = 1 h 23 min; SD = 1 h 05 min; N = 71). When more than two trips per day were recorded the mean time between the flights ranged from 30 min to 2 h 13 min (N = 7). *Bembecinus hungaricus* is a progressive provisioner and excavated nests contained 2 to 10 prey specimens. The number of prey brought into the nest per female and day varied from 1 to 10 (mean = 3.2; SD = 2.2; N = 31). The prey consisted of leafhoppers of the family Cicadellidae which were taken to the nest in low flights. The wasps flew to their assumed hunting ground, an adjacent area where young *Populus nigra* and *Salix* sp. trees were abundant, but the prey collecting was never observed. The prey was completely paralysed and carried venter up and head to head beneath the wasp's body. During the flight the leafhopper was held with the hind and middle legs.

Male behaviour

Males of *B. hungaricus* emerged before any females but only a total 13 specimens were recorded and they were only active for 5 weeks. In the first hours of daylight

they fed on honeydew on *Pinus sylvestris*. In the morning, males flew repeatedly straight over the colonies and searched for emerging females. This behaviour differentiated them from the females hovering in zigzag lines while they searched for their nests or appropriate nesting sites. During the day, males were seen at the colonies, but also visited adjacent plants where they sucked nectar on various blossoms. They attempted to mate with every encountered female and occasionally tried to mate with females of *Harpactus elegans* which nested nearby. They alighted on elevated places like plants or branches, cleaned themselves and seemed to take such sites as vantage points. They also showed aggression toward each other, pouncing together whenever they met. In late June, two males were seen at site B, patrolling along the colony. In the following months neither male nor female *B. hungaricus* were found at this site, perhaps because emerged females as well as males changed their nesting site and left this location.

Parasites

Several potential parasites were detected in the study area. Many miltogrammine flies (Diptera, Sarcophagidae) were found on the hot sand, where they inspected the entrances of open burrows and entered them. They were active during daylight and even under muggy weather, when *B. hungaricus* remained inactive. The satellite flies *Senotainia albifrons*, *Metopia* cf. *campestris* and *Paragusia elegantula* pursued prey-laden wasps to their nests. Mostly two flies accompanied a wasp, waited in flight behind until *B. hungaricus* opened the nest. The satellite flies entered the burrow directly after the wasp. They never contacted the wasp's prey in flight apparently, reaching the leafhopper prey in the burrow. This was the only opportunity for the oviposition on the prey because *B. hungaricus* closed the entrance immediately after provisioning. The only time nests were left open was during cleaning, which was never done after provisioning but rather after controlling. The flies seemed to be attracted by prey-carrying wasps and used dry plants and the marker-toothpicks as vantage points. On some occasions the wasps were seriously disturbed by the flies making diversionary flights over the nesting area or through the vegetation, that consistid of erratic movements to elude the pursuing flies and needed up to 4 escape flights to get rid of the parasites. Once (26 August 1999) a fly was seen digging the entrance free and entering the burrow after the female wasp had left. The bombyliid fly *Bombylius cinerascens* (Diptera, Bombyliidae) sometimes deposited eggs in the sand in the middle of the colonies. Nest excavations were not performed in this study in order not to disturb the population.

Habitat preferences

Bembecinus hungaricus inhabited bare sand sites with sparse vegetation (< 25 % cover). Sites with denser vegetation cover (sites B and C) were left, and loose, bare

substrates (site D) were colonised rapidly. Areas with a higher coverage were frequently used by *Bembecinus tridens*, but never by *B. hungaricus*. The size distribution of sand grains was determined at all observed sites. There were no differences between the soil particle distribution in 1998. In 1999, however, the bulldozed sandpit (site D) showed fractions of coarser grained sand with a diameter of 6.3 - 2.0 mm, whereas the sand at all other sites never exceeded a grain sizeces in the range of 0.63 - 0.02 mm.

Discussion

Bembecinus hungaricus exhibits the behavioural traits of the genus as outlined by EVANS (1955). This species conforms with *Bembecinus tridens* (KARSAI 1989) and *Bembix rostrata* (SCHÖNE & TENGÖ 1992) in showing highest activity under high temperatures and high insolation. As *B. hungaricus* is a small sized species, individuals can remain active during highest temperatures (KÄPYLÄ 1974). Furthermore wasps increase convective heat loss by speeding up in flight at high air temperatures (HEINRICH 1989).

Daily activity patterns are performed constantly but can respond immediately to temperature changes, especially before the onset of rain (NACHTIGALL 1983, STONE et al. 1988, STONE 1994): nests are inspected in the morning hours, provisioning occurs from the start of activity in the morning until the females start digging sleeping burrows. *Bembecinus hungaricus'* provisioning activity did not stop at a certain temperature maximum as reported for *Steniolia longirostra* by LARSSON (1990), but provisioning females also were recorded at the hottest hours of the day.

Like its congeners (EVANS 1955, LÜPS 1973, GESS & GESS 1975), *B. hungaricus* practised progressive provisioning and foraged during all daylight hours. The use of Cicadellidae as prey is also widespread in the genus (EVANS & MATTHEWS 1974).

The uniqueness in the behaviour of *B. hungaricus* is expressed through its behaviour during the night. Progressive provisioners and especially the genus *Bembecinus* usually spend the night away from the nest (EVANS 1955, EVANS et al. 1986). *Bembecinus hungaricus,* in contrast, digs separate sleeping burrows, which are only used once. Some *B. tridens* spend the night in burrows, but these sleeping holes are nests in which digging continues on the next day (LÜPS 1973). The same author assumed that most females slept in clusters on the vegetation. As Drösing is close to the northern limit of the species *B hungaricus* range and temperatures were low at night, plunging once to 3.1 °C, the wasps seem to prefer the more stable soil environment, where the lowest recorded temperature was 15.8 °C. Remaining in nests under cool conditions in the morning hours was also reported in *Alysson conicus* and like this species females of *B. hungaricus* became active in a few seconds when removed from their nests (O'BRIEN & KURCZEWSKI 1982).

Only a few males were found at the colonies and no copulation was observed. Due to the early disappearance of males in the course of summer it can be assumed that

all nesting females in Drösing were fertilized directly after emergence in the first two weeks of July although SCHMIDT & WESTRICH (1983) found male *B. hungaricus* in mid-August or that they were laying unfertilized eggs from which males would develop. Proterandry in the genus has also been described for *B. neglectus* (EVANS 1955) and *B. quinquespinosus* (O'NEILL & EVANS 1983) and is common within the Sphecidae (FREEMAN 1981, HASTINGS 1989). In contrast to EVANS & O'NEILL (1986), who found hundreds of active males of *Bembecinus nanus strenuus,* the number of male *B. hungaricus* was low. Less than 20 males were observed at the colonies and they probably disappeared immediately after a short mating period in July. In *B. tridens* LÜPS (1973) reports a lower temperature optimum for males than for females. This may also be true for *B. hungaricus*, because the disappearance of males coincided with increasing temperatures early in the season.

Wasps were pursued by satellite flies under all weather conditions. The flies were more attracted to prey-laden wasps than to digging females without leafhoppers Escape flights performed by female *B. hungaricus* were only moderately effective in eluding satellite flies because the flies are usually able to follow the wasps due to their enlarged eyes and facets (SPOFFORD & KURCZEWSKI 1992). Unfortunately no data on the actual frequency of cell parasitism are available for the genus *Bembecinus*, but the frequent occurrence of parasites at the nesting sites may be also responsible for the dense nesting of *B. hungaricus* in Drösing (see also LARSSON 1986).

In Drösing the thermophilic *B. hungaricus* (SCHMID-EGGER & NIEHUIS 1997) occurs only at sites consisting of bare sand. These open habitats are characterized by higher soil temperatures than areas with dense vegetation (HONEK 1988). *Bembecinus hungaricus* tends to nest at sites which are fully insolated throughout the day. Nesting sites B and C, where coverage increased mainly by growth of *Calamagrostis epigejos* from 1998 to 1999, were abandoned by the wasps in the second year of observation. This response was probably caused by an altered temperature regimes due to denser vegetation, as it has been reported for *Ammophila insignis* (WEAVING 1989). No recently emerged females were found at sites B or C either in 1999. Therefore, high nest site fidelity, as reported for *B. tridens* by LÜPS (1973) and *Halictus rubicundus* by POTTS & WILLMER (1997), could not be verified for *B. hungaricus.* Rather, females show to be rapid colonizers (sensu EVANS 1975) of sites with bare fine-grained substrate without vegetation, but do not change these nesting sites regularly every year. Unfortunately no data were collected on the microclimatic changes at sites B and C which could be responsible for the shift of nesting sites (EVANS et al. 1986).

Females of *B. quinquespinosus* change their nesting sites in response to harassment by males (EVANS et al. 1986), whereas *B. hungaricus* males did not show aggressive behaviour towards females. Furthermore, sites B and C were abandoned in mid-July 1998 after some nests had already been fully provisioned and males were no longer present.

In summary, except the daily digging of sleeping holes, which was reported for the first time for any *Bembecinus*, *B. hungaricus* possesses the behavioural features exhibited by other species of the genus.

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