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A sleeping aggregation of *Amegilla quadrifasciata maderae* (Hymenoptera, Anthophila) – with general remarks on sleeping aggregations in Hymenoptera taxa

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With 1 figure

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ABSTRACT: A photo documentation of a sleeping aggregation of *Amegilla quadrifasciata* (Villers, 1789) subspecies *maderae* (Sichel, 1867), endemic to the Madeira Archipelago, is presented. About 40 males rested together on withered twigs of *Ageratina adenophora* (Asteraceae), attached to stems by their mandibles. Many specimens had the body slightly angled horizontally or stretched out slightly curved, with the legs positioned near the body, the wings closed over the abdomen, and the antennae slightly bent backwards. The individuals were concentrated close together and formed a clumped aggregation.

The phenomenon of sleeping aggregations, their occurrences, the physiological knowledge of aggregations, behaviour at the roost, and the structure and size of aggregations, as well as the reasons for this phenomenon, are introduced with general remarks about this phenomenon.

Keywords: *Amegilla*, Anthophoridae, digger bee, Madeira Archipelago, aggregation of males, roosting, solitary bees, sleeping behaviour.

RESUMO: Apresenta-se documentação fotográfica de uma agregação de machos adormecidos de *Amegilla quadrifasciata* (Villers, 1789) subespécie *maderae* (Sichel, 1867), endêmica do Arquipélago da Madeira. Cerca de quarenta machos repousavam juntos em galhos murchos de *Ageratina adenophora* (Asteraceae), presos aos caules pelas mandíbulas. Muitos exemplares apresentavam o corpo ligeiramente inclinado na horizontal ou estendido, ligeiramente curvado, as patas posicionadas junto ao corpo, as asas fechadas sobre o abdómen e as antenas ligeiramente dobradas para trás. Os indivíduos concentravam-se próximos uns dos outros e formavam uma agregação amontoada.

O fenómeno das agregações de indivíduos adormecidos, as situações em que ocorrem, o conhecimento fisiológico, o comportamento no “poleiro”, a estrutura e dimensão das agregações, assim como as razões para o mesmo acontecer são discutidas na generalidade.

Palavras-chave: *Amegilla*, Anthophoridae, abelha escavadora, arquipélago da Madeira, agregação de machos, abelhas solitárias, comportamento de dormir.

INTRODUCTION

On 10 September 2022, a sleeping aggregation of *Amegilla quadrifasciata maderae* (Sichel, 1867), endemic to the Madeira Archipelago (KRATOCHWIL *et al.*, 2018, 2022), was detected for the first time with about 40 males resting on dried stems of *Ageratina adenophora* (Asteraceae) on Madeira Island (Fig. 1). Although sleeping aggregations have been reported in other species of the genus *Amegilla* (BANKS, 1902; RAYMENT, 1935; ALDINI, 1994; YOKOI & WATANABE, 2014; YOKOI *et al.*, 2014, 2016; SANDEEP & MUTHURAMAN, 2018), this is the first published record of an *A. quadrifasciata* aggregation.

The phenomenon of sleeping aggregations is widespread in insects and is found especially within Hymenoptera taxa (FIEBRIG, 1912; FRISCH, 1918; BISCHOFF, 1927; GRASSÉ, 1942; EVANS & LINSLEY, 1960; LINSLEY, 1962; DAFNI *et al.*, 1981; WESTRICH, 1990; KAZENAS & TOBIAS, 1993; O’NEILL, 2001; KLEIN, 2003; WCISLO, 2003). The specific types of sleeping behaviour in the different hymenopteran taxa, concerning the fixation to a substrate (mandibles, legs) and the orientation of the body (position of the head, thorax, abdomen, antennae), are highly diverse. Species-specific differences in these features also occur within a genus. Individuals may furthermore form linear or clumped aggregations. The roosting sites are often visited regularly over a longer time period, and, in some cases, there is a certain degree of site fidelity of specimens to plant species, individuals, or twigs (SCHREMMER, 1955; KAISER, 1995; ALCOCK, 1998; OLIVEIRA & CASTRO, 2002; WCISLO, 2003; ALVES-DOS-SANTOS *et al.*, 2009; SILVA *et al.*, 2011; SANDEEP & MUTHURAMAN, 2018). The phenomenon of sleeping aggregations within the Hymenoptera is discussed in detail.¹

Background: *Amegilla quadrifasciata maderae* and the observed aggregation

Taxonomic and ecological characterization of *Amegilla quadrifasciata maderae*

Amegilla quadrifasciata (Villers, 1789) has a wide transpalearctic distribution and, according to SCHEUCHL & WILLNER (2016), occurs from the Canary Islands and Portugal – via North Africa, Southern and Eastern Europe, Ukraine, and Southern Russia – to Siberia. Furthermore, via Asia Minor, Caucasus, Central Asia, Northern China, and Mongolia, it reaches Japan. In Europe, its northern distribution border reaches Luxembourg, Germany, Poland, and Ukraine. In the south, *A. quadrifasciata* occurs in Sudan, Ethiopia, and Yemen and reaches Northern India.

Amegilla quadrifasciata maderae (Sichel, 1868) is an endemic subspecies of the Madeira Archipelago. SICHEL (1868) described *A. maderae* as a separate species. The species status was accepted by ALFKEN (1940). DOURS (1869), on the other hand, regarded the specimens from the Madeira Archipelago only as a variety (*maderae*) of *A. quadrifasciata*. LIEFTINCK (1956, 1958) also assigns the specimens from the Madeira Archipelago to *A. quadrifasciata*. According to KRATOCHWIL *et al.* (2022), it is a

¹ All taxa names used in this publication were checked for validity by A. K.; for this purpose, many older publications were evaluated. Only the names that are valid today were used, and synonyms were corrected. As these are valid names, we did not add the names of the authors for reasons of space and better reading.



Fig. 1 – Sleeping aggregation of males of the digger bee *Amegilla quadrifasciata maderae* (Sichel, 1867); Eira da Achada (Ribeira da Janela), 10 September 2022, 7 pm, observed and photographed by Neide Gouveia. Males with orange-red and with yellowish abdominal bands occur.

subspecies of *A. quadrifasciata*, which can be classified as a melanistic form of the nominate taxon. In addition to the black to dark brown pubescence of the head and thorax, *A. q. maderae* has orange-reddish to yellowish tergite hair bands in contrast to the nominate form, which has light brownish thoracic hairs and whitish to white hair bands. In *A. quadrifasciata*, the tergite hair bands are as wide as the tergite depression; in *A. q. maderae*, the hair bands are much narrower. The genital morphology is not different from that of the nominate taxon, and a molecular genetic investigation confirms the affiliation to one species (KRATOCHWIL, *unpublished*).

Amegilla q. maderae is a typical bee species of the dry, lower subhumid vegetation stages of the island Madeira (KRATOCHWIL *et al.*, 2022). *Echium plantagineum* and *E. nervosum* are the most important pollen and nectar sources of this polylectic species (KRATOCHWIL *et al.*, 2022). *Amegilla q. maderae* flies all year round. The colonies of this ground-nesting species are mostly located near larger *Echium nervosum* stands, often growing in the vicinity of cliffs. Larger *Echium* populations also act as attractors.

The sleeping aggregation of *Amegilla quadrifasciata maderae* with a comparison to other *Amegilla* species

In Eira da Achada (Ribeira da Janela, Madeira Island), a sleeping aggregation of about 40 males of *Amegilla quadrifasciata maderae* (Sichel, 1867) was detected on dried branches and twigs of *Ageratina adenophora* (Asteraceae) by Neide Gouveia on 10 September 2022 at 7 pm local time. The males had attached themselves to the twigs with their mandibles. In many cases, the body was slightly angled horizontally or stretched out slightly curved, the legs were situated near the body, the wings were closed over the abdomen, and the antennae were slightly bent backwards. The individuals were located close together and formed a clumped aggregation.

The males had different colours of the thoracic hairs and the hair bands of the tergites (Fig. 1). There were specimens with orange-yellow pubescence in the anterior part of the mesothorax, dark brown to orange-yellow pubescence in the posterior part, dark brown pubescence

on the scutellum, and orange-yellow abdominal bands. Other specimens had predominantly yellowish hairs in the thoracic region with yellow abdominal bands (Fig. 1). LIEFTINCK (1958) already mentioned that conspicuous age-related changes in the colour of the pubescence can occur in *A. quadrfasciata* (fresh individuals with vivid colours, older individuals with pale and pallid colours). Obviously, this is less related to age than to the colour polymorphism of this melanistic species, which is even more pronounced in females than in males.

The phenomenon of sleeping aggregations is well known within the genus *Amegilla* and is mentioned for the following species: *A. bombiformis* (RAYMENT, 1935), *A. cinctofemorata* (RAYMENT, 1935), *A. florea urens* (YOKOI & WATANABE, 2014; YOKOI *et al.*, 2016, 2017), *A. garrula* (ALDINI, 1994), *A. punctata* (RAYMENT, 1935), *A. salteri* (RAYMENT, 1935), *A. s. senahai* (YOKOI *et al.*, 2016), and *A. zonata* (SANDEEP & MUTHURAMAN, 2018).

As in the case of *A. q. maderae*, male aggregations predominate in *A. zonata* (SANDEEP & MUTHURAMAN, 2018) and *A. s. senahai* (YOKOI *et al.*, 2016). In *A. f. urens*, male, female, and mixed aggregations exist (YOKOI & WATANABE, 2014; YOKOI *et al.*, 2016, 2017).

As a rule, the females spend the night in their nests, so the occurrence of females in aggregations is rather rare. The males search for overnight quarters (*e.g.*, flowers, protected areas in cavities, holes in branches they dig themselves). In the case of *A. florea urens*, the females already had mature eggs (YOKOI & WATANABE, 2014; YOKOI *et al.*, 2016). The females of *A. f. urens* do not spend the night in the nests but in a sleeping aggregation similar to that of the males. During the day, they are busy nest building and provisioning the nests with pollen, which is completed in the evening with one egg per cell.

In *A. zonata*, these aggregations have a size of 2-25 individuals (SANDEEP & MUTHURAMAN, 2018). Accordingly, the aggregation of *A. q. maderae* is quite large. A prerequisite for the size of a sleeping aggregation is the existence of large nest aggregations with large populations in the vicinity. However, such large populations do not occur frequently in the Madeira Archipelago. Individual-rich nesting colonies were found at Ribeira Brava (Miradouro do Pico da Cruz), near Cabo Girão, and near Porto Moniz. The largest nesting population was found on Porto Santo at Ponta da Calheta with about a hundred nests (KRATOCHWIL & SCHWABE, personal observation). Other aggregations occur south of Pico do Facho.

Sleeping aggregations of *A. zonata* were found at one and the same site for 45 days (SANDEEP & MUTHURAMAN,

2018). On one plant, several aggregations (with a maximum of eight clusters) could be present per branch (stem, twig) (SANDEEP & MUTHURAMAN, 2018). In a few cases, other bee species (*e.g.*, *Thyreus*, *Megachile*) were also found on the roosting site of *A. zonata*. In *A. f. urens* and *A. zonata*, the sleeping aggregations were arranged linearly on branches or leaves (MIYANAGA *et al.*, 2011; YOKOI & WATANABE, 2015; YOKOI *et al.*, 2016, 2017; SANDEEP & MUTHURAMAN, 2018). This phenomenon is also found in other wild bee species, such as *Anthophora plumipes* (PITTIONI, 1933). In *A. q. maderae*, however, it was a clumped (ball-like) aggregation. The fixation of *A. q. maderae* individuals on plant stems resembles that of *A. f. urens*, with the specimens holding on only with the mandibles, the legs leaning against the body, and the antennae stretching forwards or leaning sideways.

General view of the phenomenon of sleeping aggregations in insects, especially in Hymenoptera

The phenomenon of sleeping communities in Hymenoptera – early historical observations

LINNAEUS (1758) already pointed out sleeping bees and even named a species *Apis florisomnis* ('per noctes floribus inhaerens') sleeping in flowers, which today has the name *Chelostoma florisomne* (Linnaeus, 1758). The first evidence of aggregative sleeping behaviour in Hymenoptera is found in WESTWOOD (1840) on scoliids (*Scolia galbula*, *S. sexmaculata*), with the observation of aggregations of 20-30 individuals. Early observations of insect sleeping are described by HILL (1865) and CRESSON (1872). FRIESE (1891) mentioned the phenomenon in *Trachusa byssina*. KEARLY (1857) described an observation of sleeping males of *Chelostoma florisomne* without, however, referring to LINNAEUS (1758). SNELLEN VAN VOLLENHOVEN (1858) discovered a sleeping aggregation of *Colletes succinctus* (species determination corrected by RITSEMA, 1879).

Probably the first reference to sleeping wild bees (*Thyreus*), fixed with mandibles, is mentioned by GUEINZIUS (1858); another reference, without naming the species or the genus, is given by NEWMAN (1859). FABRE (1879) described an aggregation with hundreds of specimens of the sphecid *Podalonia hirsuta* and described the sleeping behaviour of the sand wasp *Ammophila heydenii* (FABRE, 1897). The first record of sleeping solitary bees is given by CRESSON (1865) on the cuckoo bee *Mesoplia rufipes*. Early data on sleeping aggregations are found in PÉREZ (1889), FRIESE (1891, 1899, 1908, 1923), VERHOEFF (1892), SAUNDERS (1896),

SCHWARZ (1896), BANKS (1902), BRUES (1903), LÜDERWALDT (1910), FIEBRIG (1912), and RAU & RAU (1916). FIEBRIG (1912) provided the first comprehensive overview of the phenomenon and included a tabulation of the taxa for which sleeping communities had been observed.

Structure of sleeping aggregations, preferences, and behaviour

In wild bees, but also in many other hymenopteran taxa, large aggregations of sleeping individuals may occur outside the nest. These aggregations are named 'sleeping aggregations' or 'roosting aggregations' (EVANS & LINSLEY, 1960; LINSLEY, 1962; O'NEILL, 2001; AZEVEDO & FARIA, 2007). Usually, an aggregation is built by one species and one sex, in most cases by males. However, there also exist female aggregations and mixed aggregations (males, females) at one roost site.

Sleeping aggregations characterized by one species

In solitary wild bee species, aggregations with only males are commonly found within different bee families:

- **Colletidae:** *Colletes meridionalis* (SCHROTTKY, 1922), *Hylaeus* (BISCHOFF, 1927).
- **Andrenidae:** *Panurginus labiatus* (PITTIONI & SCHMIDT, 1943), *Parapsaenythia paspali* (SCHROTTKY, 1922).
- **Anthophoridae:** *Amegilla s. senahai* (YOKOI *et al.*, 2016), *A. zonata* (SANDEEP & MUTHURAMAN, 2018).
- **Apidae:** *Anthophora crassipes* (FIEBRIG, 1912), *Centris flavifrons*, *C. leprieuri* (GOTTSBERGER *et al.*, 1988), Eucerini (MAHLMANN *et al.*, 2014), *Euglossa melanotricha* (SILVA *et al.*, 2011), *Melissodes* (SCHROTTKY, 1922; MATHEWSON & DALY, 1955).
- **Halictidae:** *Augochlorella neglectula* (WCISLO, 2003), *Augochloropsis anesidora* (SCHROTTKY, 1922), *Lasioglossum* (FRISCH, 1918; SCHREMMER, 1955; MIYANAGA & MAETA, 1998), *Neocorynura oiospermi* (SCHROTTKY, 1922).
- **Megachilidae:** *Dianthidium gregarium* (SCHROTTKY, 1922), *Epanthidium bertonii* (SCHROTTKY, 1908, 1922), *Hypanthidium flavomarginatum* (FIEBRIG, 1912), *Megachile curvipes* (FIEBRIG, 1912).

Male sleeping aggregations are found not only in solitary species but also in social wild bee species, e.g., in stingless bees of the genus *Tetrapedia* (*T. diversipes*) (FIEBRIG, 1912; SCHROTTKY, 1922; ALVES-DOS-SANTOS *et al.*, 2002, 2009; SANTOS *et al.*, 2014), in *Frieseomelitta varia* (SARAVANAN, 2005;

SANTOS *et al.*, 2014), and in bumblebee species (e.g., *Bombus dahlbomii*; JOSEPH, 1929).

Male aggregations also occur in Scoliidae, e.g., *Colpa quinquecincta* (RAU & RAU, 1916), and Vespidae (EVANS & LINSLEY, 1960), e.g., *Antepipona bipustulata* (RAJMOHANA, 2018).

Mixed male and female sleeping aggregations are rarer (e.g., *Anthophora montana* and *A. urbana*; LINSLEY, 1962) and were detected in Scoliidae and Sphecidae (EVANS & LINSLEY, 1960).

Female sleeping aggregations have been observed in *Coelioxys afra*, *C. conoidea*, and *Nomada flavopicta* (SCHREMMER, 1955; FREEMAN & JOHNSTON, 1978; YOKOI & WATANABE, 2015). Aggregations with only females exist in *Coelioxys praetextatus* and *Paratetrapedia nigripes* (FIEBRIG, 1912). In *Lasioglossum sisymbrii*, non-nesting females are also found to form roosting societies on dry stems, often together with individuals of the genera *Agapostemon* and the potter wasp *Stenodynerus* (LINSLEY, 1962).

In mixed aggregations, the sexes exhibit different behaviour. Females of *Amegilla f. urens* arrive at the roost later and leave it earlier in the morning than males (YOKOI & WATANABE, 2015). This suggests that females use the roost regularly and avoid staying longer together with males. The use of the same roost by the two sexes could be due to the limited number of suitable roosts in the forest ecosystem (YOKOI & WATANABE, 2015). But roosts also serve for mating in mixed aggregations, e.g., in *Svastra obliqua* (EVANS & GILLASPY, 1964).

HAUSL-HOFSTÄTTER (2004) assumed that in the case of single resting females (e.g., *Anthidium septemspinorum*) in male communities, the females are those that have completed nest-building activity. EVANS & LINSLEY (1960) indicated that in species that do not build nests (e.g., *Scolia*) or that are brood parasites (e.g., *Nomada*, *Triepeolus*), both sexes are more likely to occur at roosts.

Sleeping aggregations characterized by several species

There are also multispecies sleeping aggregations (BANKS, 1902; RAU & RAU, 1916; EVANS & LINSLEY, 1960; LINSLEY, 1962). RAU & RAU (1916) found three species at one roost (*Melecta obscura*, *Melissodes bimaculata*, *M. veroniana*). It is possible to divide multigenus aggregations into those in which representatives of only one genus occur. An example is the aggregation of the two sphecids *Chalybion californicum* and *C. z. zimmermanni* (LANDES & HUNT, 1988). Examples in which representatives of different bee genera form sleeping aggregations are, however, more common.

RAYMENT (1935) found the following species on one branch: *A. cinctofemorata*, *A. punctata*, and *A. salteri*, as well as 300 males of the genera *Nomia*, *Paracolletes* and *Stenotritus*. Aggregations with other hymenopteran taxa also occur. BRUES (1903) found five bee and wasp species sleeping on a *Melilotus* plant. EVANS & LINSLEY (1960) detected 21 wasp and 15 bee species on *Melilotus*, together with three *Ammophila* species, which dominated in number of individuals. The wasp species included species of Crabronidae, Scoliidae, Sphecidae, and Vespidae, while the bee species included species of Apidae, Megachilidae, and Halictidae.

Different behaviour of species on roosting sites has been observed. BRADLEY (1908) and EVANS & LINSLEY (1960) described separate species-specific areas within mixed roosting aggregations. The roosting species show different patterns of occurrence. EVANS & LINSLEY (1960) distinguished regularly occurring species (regulars), irregularly occurring species (irregulars), and occasionally occurring species (casuals). The different sleeping species form their own clusters within the overall aggregation; the species do not mix.

In mixed aggregations, there are also cases in which hosts and their parasites rest together at the same roost. LINSLEY & McSWAIN (1958) reported this phenomenon for *Colletes* and *Epeolus*, and SANDEEP & MUTHURAMAN (2018) detected interspecific aggregations with individuals of *Megachile* and *Thyreus*.

There are also 'daytime aggregations' with mixed aggregations of females and males of *Centris decolorata*, *C. lanipes*, and *C. smithii* (STARR & VELEZ, 2009) and with the pompilid *Pepsis sericans* (STARR & HERNANDEZ, 1995).

A particular case is the co-occurrence of *Amegilla f. urens* and butterflies in the same resting place (YOKOI & WATANABE, 2014). LINSLEY (1962) described mixed aggregations with hymenopterans and wasp-like dipterans (Conopidae, Stratiomyidae, Syrphidae), as well as with tachinids and even hemipterans.

Aggregation shapes

In wild bees, loose, dense (ball-like), and linear aggregations can be distinguished (EVANS & LINSLEY, 1960; HAUSL-HOFSTÄTTER, 2004, 2008):

- Loose aggregations:

Antepipona bipustulata (RAJMOHANA, 2018), *Anthidiellum robertsoni* (LINSLEY, 1962), *A. strigatum* (SCHREMMER, 1955; CARAYON, 1967; WESTRICH *et al.*, 1992), *Anthidium septemspinum* (HAUSL-HOFSTÄTTER, 2004), *Anthophora*

urbana (LINSLEY, 1962), *Augochlorella neglectula* (WCISLO, 2003), *Biastes emarginatus* (WESTRICH *et al.*, 1992), *Hylaeus* spec. (BISCHOFF, 1927; GEISER, 1988), *Macropis europaea* (LIEFTINCK, 1957; WESTRICH *et al.*, 1992), *Mellisodes paroselae* (LINSLEY, 1962), *M. tristis* (LINSLEY, 1962), *Nomia* spec. (LINSLEY, 1962; GEISER, 1988; BLÖSCH, 2006), *Nomia melanderi* (STEPHEN *et al.*, 1969).

- Dense aggregations:

Centris xanthomelaena (MARTINS *et al.*, 2018), *Eucera nigrescens* (PEETERS, 2012), *Frieseomelitta varia* (SANTOS *et al.*, 2014), *Lasioglossum albipes* (SCHREMMER, 1955), *L. calceatum* (SCHREMMER, 1955), *L. fratellum* (Schremmer, 1955), *Melitta leporina* (WESTRICH *et al.*, 1992), *M. nigricans* (PEETERS, 2012), *Melissodes* aff. *bonaerensis* (MAHLMANN *et al.*, 2014), *M. denticulatus* (MATHEWSON & DALY, 1955), *M. nigroaenea* (SCHROTTKY, 1922; MAHLMANN *et al.*, 2014), *Nomia foxii* (EVANS & LINSLEY, 1960), *N. strigata* (LIEFTINCK, 1957), *Oxaea austera* (OLIVIERA & CASTRO, 2002), *Svastra duplocincta* (ALCOCK, 1998), *Tetrapedia diversipes* (ALVES-DOS-SANTOS, 2009).

- Linear aggregations:

Amegilla zonata (SANDEEP & MUTHURAMAN, 2018), *Svastra duplocincta* (ALCOCK, 1998).

There are similar examples in wasps (EVANS & LINSLEY, 1960; GILLASPY, 1963; EVANS, 1966):

- Small groups with both sexes:

Bicyrtes, *Stizoides*.

- Loose clusters:

Ammophila (EVANS & GILLASPY, 1964), *Bicyrtes capnopterus* (GILLASPY *et al.*, 1962), *Stictiella pulchella* (EVANS & GILLASPY, 1964), *Stizoides renicinctus* (GILLASPY, 1963).

- Dense clusters with both sexes:

Bembecinus quinquespinus, *Glenostictia pulla*, *Rubrica*, *Stictiella*, *Svastra*, *Zyzzys chilensis* (EVANS, 1955; EVANS & GILLASPY, 1964).

- Dense clusters of males:

Glenostictia scitula (GILLASPY *et al.*, 1964).

- Linear aggregations:

Celonites abbreviatus (AMIET & MAUSS, 2003).

Size of the aggregations

A sleeping aggregation can contain up to 1000 individuals (BRAUNS, 1911; RAU & RAU, 1916; DEEGENER, 1918; LINSLEY & CAZIER, 1972; ALCOCK, 1998; MAHLMANN *et al.*, 2014). Aggregations of up to 50 sleeping individuals were found in *Anthidium septemspinum* (HAUSL-HOFSTÄTTER, 2004). Aggregations of up to 1000 individuals were observed in

the crabronid wasps *Bembecinus* and *Bembix* (BLÖSCH, 2000; MAHLMANN *et al.*, 2014).

Numerous species show site fidelity (SCHREMMER, 1955; KAISER, 1995; ALCOCK, 1998; OLIVEIRA & CASTRO, 2002; WCISLO, 2003; ALVES-DOS-SANTOS *et al.*, 2009; SILVA *et al.*, 2011; SANDEEP & MUTHURAMAN, 2018). Individuals can occur at the same site for a few days to several months (EVANS & LINSLEY, 1960; THOENES, 1994; ALCOCK, 1998), and even completely different generations can use the same site for several years (LINSLEY, 1962; EVANS, 1966). SILVA *et al.* (2011) observed male roost aggregations of *Euglossa melanotricha* at the same locality for over a year. SANDEEP & MUTHURAMAN (2018) described site fidelity for *Amegilla zonata*, ALCOCK (1998) for *Svastra duplocincta*, and WCISLO (2003) for *Augochlorella neglectula*.

Usually, aggregations are found at the branch ends, *e.g.*, in *Tetrapedia diversipes* (ALVES-DOS-SANTOS *et al.*, 2009). A distinction should be made between site fidelity to individual plants and site fidelity to individual branches (HAUSL-HOFSTÄTTER, 2004). There is also temporary fidelity to a roost site (HAUSL-HOFSTÄTTER, 2004). However, some species have no site fidelity (WESTRICH *et al.*, 1992).

Characterization of the sleeping sites

Males of Hymenoptera taxa spend the night on plant branches, on leaves, in cavities, in the ground in self-dug roost nests, or in flowers (MIYANAGA & MAETA, 1998; WCISLO, 2003; BLÖSCH, 2006; SASAKI & SASAKI, 2008; ALVES-DOS-SANTOS *et al.*, 2009; MAHLMANN *et al.*, 2014; SABINO *et al.*, 2017). However, dried fruits and bird nests are also used (AZEVEDO & FARIA, 2007). In contrast, females usually roost within their nests, which is interpreted as predator protection (AGUIAR & GAGLIANONE, 2003; MARTINS *et al.*, 2014). Both FRIESE (1923) and LINSLEY & CAZIER (1972) mentioned that females do not form roost aggregations outside the nest, but this is not true, as this phenomenon had already been described by FIEBRIG (1912). SCHREMMER (1955) observed females and males of *Anthidiellum strigatum*, *Anthidium punctatum*, and *Trachusa byssina* sleeping on plants, but usually females occurred in lower numbers.

MARTINS *et al.* (2014) mentioned that *Centris xanthomelaena* also has females roosting outside their nests, forming mixed roosting communities with males. This also occurs in *C. burgdorfi* (SABINO *et al.*, 2017).

Roost sites are often branches, twigs, or stems (FREEMAN & JOHNSON, 1978; ALCOCK, 1998). Among bees, the so-called stalk sleeper includes species of the genera *Dasypoda*, *Lasioglossum*, *Macropis*, *Nomia*, *Tetralonia*, and *Trachusa* (BLÖSCH, 2006).

There is a preference for resting places characterized by many branches or twigs, by structurally rich, dead, and dry plants with a height of about 90-180 cm, and by sufficient morning and evening sun (LINSLEY, 1962). However, fresh plants are also used (BANKS, 1902; MATHEWSON & DALY, 1955; LINSLEY & MACSWAIN, 1958; LINSLEY, 1962; BIERI, 2002; OLIVEIRA & CASTRO, 2002; HAUSL-HOFSTÄTTER, 2004).

LINSLEY (1962) described different location preferences of Hymenoptera species in multiple aggregations on a plant. Three different *Ammophila* species (Sphecidae) preferred approximately vertically oriented branches in the centre of the plant at a height of 0.6 to 1.2 m, whereas species of the genus *Bicyrtes* (Crabronidae) preferred horizontal branches at the same height but in the outer parts of the plant. The top of the plant (at a height of 1.2 to 1.7 m) was used by species of the genus *Prionyx* (Sphecidae) and by scoliids. Males of *Agapostemum angelicus* (Halictidae), *Bicyrtes capnopterus* (Crabronidae), *Euodynerus cf. annulatus*, and *E. cf. hildago* (Vespidae) preferred exclusively dry inflorescences. Other vespids were found at various branch ends at a height of 0.9 m, and bees resided below *Ammophila* species. Species that used the roost only irregularly and occasionally tended to be on the outer areas of the plant.

Nevertheless, living plants also serve as resting places (BANKS, 1902; MATHEWSON & DALY, 1955; LINSLEY & MACSWAIN, 1958; LINSLEY, 1962; BIERI, 2002; OLIVIERA & CASTRO, 2002).

Preferred habitats are ruderal sites (HAUSL-HOFSTÄTTER, 2008). *Amegilla zonata* preferred roosts near food plants (SANDEEP & MUTHURAMAN, 2018). Suitable roost sites are limited (WESTRICH *et al.*, 1992).

Approach, preferences, and behaviour at the roosting site

The specimens usually find each other in the late afternoon or early evening (LINSLEY, 1962). SANDEEP & MUTHURAMAN (2018) gave the time before sunset for *Amegilla zonata*. HAUSL-HOFSTÄTTER (2004) observed search flights of *Anthidium septemspinum* near the later roosting place. Some individuals settled on shrubs, grasped a branch with their legs, and bit down with their mandibles, but then left the site again. Stems where other bees had already settled were highly attractive (ALCOCK, 1998; HAUSL-HOFSTÄTTER, 2004). Already settled specimens, which had not yet reached the roosting state, changed their location again (HAUSL-HOFSTÄTTER, 2004). During the approach, already sitting individuals were often attacked (HAUSL-HOFSTÄTTER, 2004).

If the attack was successful, the 'victor' would settle at that location. Often, however, there was also a successful defense by the attacked specimen (HAUSL-HOFSTÄTTER, 2004).

In *Svastra duplocincta*, a preference has been demonstrated for the uppermost parts of a branch as a resting place (ALCOCK, 1998). This has also been observed by HAUSL-HOFSTÄTTER (2004) for *Anthidium septemspinosum*, and SCHREMMER (1955) mentioned that *Anthidium* always fixes itself at the uppermost branch end. In this genus, there is even a fight for the uppermost position at the roost analogous to the territorial behavior in *A. septemspinosum* (SUGIURA, 1991).

Distinct clusters of roosting specimens can be formed on a plant. Some areas are used by sleeping individuals, but others remain unoccupied.

Individuals may show a high preference for a single plant and even for individual stems (PITTIONI, 1933; CARAYON, 1967; ALCOCK, 1998; MARTINS *et al.*, 2018; SANDEEP & MUTHURAMAN, 2018). These preferences were supported by experiments conducted by ALCOCK (1998). At short distances, visually perceived factors play a role (WCISLO, 2003). Scent markings previously left by males at roost sites are likely responsible for these preferences (ALCOCK, 1998; WCISLO, 2003). For example, *Andrena* males mark leaves, petioles, grass blades, or buds along their flight paths with scents from the mandibular gland (MÜLLER, 1991; MÜLLER *et al.*, 1997). Male bumblebees use labial gland secretions for flight path marking of their territories (ALFORD, 1975). BRUES (1906) already reported on preferences for certain plant species. He found *Scolia cf. lecontei* only on Apiaceae.

In multispecies roost aggregations, the arrival times of species may differ. LINSLEY (1962) gave the following order:

1. Cleptoparasitic bees
(*Brachymelecta*, *Coelioxys*, *Triepeolus*).
2. Solitary bees (*Anthophora*, *Melissodes*).
3. Semisocial bees (*Agapostemon*).
4. Vespidae (*Rygchium*, *Stenodynerus*).
5. Sphecidae (*Ammophila*).
6. Sphecidae (*Eumenes*, *Prionyx*, *Sphex*).

In the morning, the specimens leave the roost in reverse order.

Fixation with the mandibles and body position

SCHREMMER (1955) pointed out that sleeping with tightly bitten mandibles in male aggregations occurs

mainly in belly collectors (Gastrilegidae), e.g., species of the genera *Anthidium*, *Heriades*, *Megachile*, *Osmia*, and *Trachusa*. However, such behaviour also exists in leg-gatherers (Podilegidae), e.g., in the genus *Tetrapedia* (*T. diversipes*, *T. peckoltii*) (FIEBRIG, 1912; BUTTEL-REEPEN, 1915; GRASSÉ, 1942; ALVES-DOS-SANTOS *et al.*, 2009).

In summary, species of the genera *Amegilla*, *Ammobates*, *Anthidium*, *Anthidiellum*, *Anthophora*, *Biastes*, *Centris*, *Coelioxys*, *Chelostoma*, *Epeoloides*, *Epeolus*, *Eucera*, *Melecta* (*Eupavlovskia*), *Nomada*, *Pasites*, *Leiopodus*, *Tetrapedia*, *Thyreus*, and *Triepeolus* fix themselves on the stem with their mandibles firmly bitten (FRIESE, 1888, 1891, 1899, 1923; FIEBRIG, 1912; SCHREMMER, 1955; WESTRICH, 1989, 1990; WESTRICH *et al.*, 1992; KAISER, 1995; MÜLLER *et al.*, 1997; ALVES-DOS-SANTOS *et al.*, 2002; HAUSL-HOFSTÄTTER, 2004, 2008; PEETERS, 2012; MARTINS *et al.*, 2018). The head is usually oriented upwards, and the rest of the body is angled horizontally (FRIESE, 1923).

In species of the genus *Amegilla*, in the roosting stage with mandibles firmly bitten, the abdomen is angled slightly horizontally (LIEFTINCK, 1957). The head is oriented upwards, and the legs and wings are near the body. *Thyreus ramosus* holds on only with the mandibles, with the legs laid on and the abdomen angled.

The head of *Epeolus variegatus* is always oriented upwards, with the legs laid out and the antennae stretched forwards (BLÖSCH, 2006). In *Anthidium septemstrigatum*, only the mandibles are fixed, the body is stretched away horizontally and only slightly angled, and the legs and wings, as well as the antennae, are densely laid out (HAUSL-HOFSTÄTTER, 2004). In *Anthidiellum strigatum*, the head is oriented downwards, the wings and legs are laid out, and the body is angled obliquely (CARAYON, 1967). In *Anthophora montana*, *A. urbana*, *Coelioxys*, *Anthidiellum*, and *Melissodes tristis*, the head is also oriented downwards. *Amegilla zonata* shows variability in this behaviour. This species also holds on with the mandibles, but the legs are either not applied or also used for holding on (SANDEEP & MUTHURAMAN, 2018).

A slight movement (even when the mandible is at rest) changes the entire position of the body. This allows the individuals to raise and lower the body during sleep (CARAYON, 1967).

Odynerus melanocephalus also holds itself with the mandibles, but it has the body curved in a U-shape and oriented in a lateral position (HAUSL-HOFSTÄTTER, 2008). Like chrysidids, the masarid *Celonites abbreviatus* curls around the stem when asleep, but this behaviour does not appear to be typical for masarids (CARYON, 1967).

Trachusa byssina orients the body with the head upwards and rests the legs (SCHREMMER, 1955). *Nomada crucis* has its head downwards (EVANS & LINSLEY, 1960), which is also generally described for *Nomada* (FRIESE, 1888, HAUSL-HOFSTÄTTER, 2008).

Species of the genus *Ammophila* bite with their mandibles (SCHREMMER, 1955; BLÖSCH, 2006). The same applies to the evaniid *Gasteruption hastator*. The head is directed downwards, and the abdomen protrudes laterally (BISCHOFF, 1927; SCHREMMER, 1955).

SCHREMMER (1955) wondered how the mandibles could hold the whole body for several hours without fatigue. BUDDENBROCK (1939) pointed out the presence of a tonic muscle that may cause this (GRASSÉ, 1942). RAYMENT (1935) reported that large raindrops can cause specimens to decapitate.

Locking with the mandibles and legs

In *Melecta obscura*, in addition to the mandibles, the first pair of legs is used for holding on, and the second and third pairs of legs are extended (HAUSL-HOFSTÄTTER, 2008). Males of *Ancyloscelis* species are fixed with the mandibles and the first two pairs of legs; the third pair of legs is spread (ALVES-DOS-SANTOS, 1999).

In *Coelioxys ruficauda*, the stem is also grasped with the mandibles and the first pair of legs, but the body is oriented with the head downwards, and the legs are attached (LINSLEY, 1958; CARRÉ & PY, 1981). The body is angled obliquely with the ventral side, and the mandibles bear the entire body weight. In *Coelioxys afra* and *C. conoidea*, the head is also oriented downwards, and the legs are laid out (SCHREMMER, 1955). In *Anthophora dalmatica*, the mandibles fix the body, the wings and legs are attached, and the antennae are directed backwards. In this species, however, the body lies directly against the stem (HAUSL-HOFSTÄTTER, 2008).

Species of the genera *Exomalopis*, *Mellisodes*, and *Svastra* hold on to the stem with all legs and the mandibles (RAU & RAU, 1916).

Ammophila fernaldi, *A. juncea*, *A. procera*, and *A. pruinosus* hold on with the mandibles and legs, with the head oriented upwards and the body angled (EVANS & LINSLEY, 1960). The eumenine *Antepipona bipustulata* holds on with the mandibles and the first pair of legs. The head is oriented upwards, and the body is parallel to the stem. The wings are folded, and the abdomen has no contact with the substrate.

Differences in locking within a genus

Within a genus, species may differ in the way they are fixed. In *Melecta duodecimmaculatum*, the second and third pairs of legs hang down, and the antennae are extended sideways at half height. In *M. leucorhyncha*, all legs are attached to the body, and the antennae are extended forwards and downwards, but in *M. albifrons* they are extended forwards and sideways. In *M. albifrons*, the specimen hangs freely in the air, except for the mandibular contact, with the legs and wings close to the body and the antennae hanging down to the side.

In the case of *Nomada ruficornis*, the abdomen hangs down (FRIESE, 1891; SCHREMMER, 1955). In *N. femoralis* and *N. integra*, the body is free in the air, except for the mandibular contact, and is slightly curved upwards, with the antennae hanging down or straight forwards (HAUSL-HOFSTÄTTER, 2008). PEETERS (2012) pointed out that there are differences in leg posture and antennal orientation (forward, backward) in *Nomada* and proved this with photos. *Nomada crucis* holds on with the mandibles, but the legs are bent freely. *Nomada flava* fixes itself with the mandibles and legs, with the head up and the antennae forwards (BLÖSCH, 2006). The head position is upward in *Anthophora bimaculata* (MÜLLER *et al.*, 1997) and *A. dalmatica* but downward in *A. montana*, *A. urbana*, and *A. smithii* (HAUSL-HOFSTÄTTER, 2008).

Even within closely related species, differences occur: *Chelostoma florissomne* fixes itself with mandibles and the first pair of legs, whereas *Osmia adunca* and *O. bicornis* do not use the mandibles but fix themselves only with the legs.

There are also differences in the position of the antennae. In individuals of *Trachusa byssina*, the antennal position varies (SCHREMMER, 1955), but in *Coelioxys afra* and *C. conoidea*, as well as in *Nomada flavopicta* and *N. ruficornis*, the antennae are always stretched straight forwards (BLÖSCH, 2006), with the head oriented obliquely upwards and the abdomen hanging down (SCHREMMER, 1955).

In *Mellisodes bimaculata*, the head is oriented upwards (BANKS, 1902, 1908), whereas in *M. denticulatus*, *M. tristis*, and *Svastra obliqua*, it is oriented downwards (FRIESE, 1923; MATHEWSON & DALY, 1955; LINSLEY, 1962). *Mellisodes* aff. *confusus* holds on with the mandibles and the legs, and *M. paroselae* only with the mandibles (EVANS & LINSLEY, 1960).

There are also differences in sleeping posture between *Ammophila heydeni* and *A. touareg*; in the latter, the body is oriented vertically (ROTH, 1928). Within the mason wasp genus *Odynerus*, the resting position also differs (BANK, 1902; FIEBRIG, 1912; HAUSL-HOFSTÄTTER, 2008).

In Sphecidae, species within a genus show differences in sleeping posture. In *Ammophila campestris*, *A. pubescense*, and *A. sabulosa*, the head is directed upwards, the legs lie loosely against the body, and the abdomen is slightly angled (GRANDI, 1961; CARAYON, 1967; BLÖSCH, 2000). In *Priononyx lividocinctus* and *P. kirbii*, the head is always directed downwards, and the legs clasp the stem (CARAYON, 1967; BLÖSCH 2000, 2006), which is also the case in *Elis sexcincta* and *Scolia lecontei* (BRADLEY, 1908). In *Prionyx parkeri*, the head is oriented downwards. In this species, arresting occurs only with the legs (EVANS & LINSLEY, 1960). BRUES (1903) also pointed out that in the wasps he studied (*Elis sexcincta*, *Nysson plagiatus*, *Scolia bicincta*, *S. lecontei*, *Tachytes*), the head was always oriented downwards. This also applies to the scoliid *Meria cylindrica* (CARAYON, 1967) and the ichneumonid *Syzeuctus fuscator* (HAUSL-HOFSTÄTTER, 2008). These species hold on with the mandibles and legs, the head is directed upwards, and the body is oriented downwards, closely following the substrate. There are also differences within a species: SCHULTZE (1924) found several resting postures in the braconid *Habrobracon hebetor*.

Locking without mandibles

There are species, such as *Andrena ovatula* (HAUSL & HOFSTÄTTER, 2008) and *Scolia dubia* (RAU, 1938), that do not use the mandible. Males of the genera *Colletes*, *Hylaeus*, *Lasioglossum*, *Macropis*, and *Melitta* are fixed only with their legs (PEETERS, 2012). However, SCHREMMER (1955) also observed locking with the mandibles in *Lasioglossum albipes*, *L. calceatum*, and *L. fratellus*. Their abdomen is directed steeply upwards, and the legs are laid out. *Scolia* is arrested only with its legs (HAUSL-HOFSTÄTTER, 2008). The ichneumonid *Syzeuctus fuscator* rests with its head down without mandibles and holds on only with its legs. The antennae are stretched straight forwards (BLÖSCH, 2006). Species of the genera *Podalonia* and *Sphex* do not use the mandibles (BLÖSCH, 2006).

Cleaning movements, pumping movements

Species of the genera *Centris*, *Epeolus*, *Protepeolus*, and *Triepeolus* show cleaning movements with the legs on the body after locking with the mandibles. Cleaning movements are also found in *Anthidium septemspinosum* and *Anthophora dalmatica* (HAUSL-HOFSTÄTTER, 2004, 2008). This is followed by pumping movements in which the thorax and abdomen arch up and down (FIEBRIG, 1912; KAISER, 1995). Pumping movements were also observed in

Amegilla zonata (SANDEEP & MUTHURAMAN, 2018) and *Anthidium septemspinosum* (HAUSL-HOFSTÄTTER, 2004). HAUSL-HOFSTÄTTER (2008) described the process of falling asleep and waking up for *Melecta obscura*. After it clings with the mandibles, the tarsi of the second and third pairs of legs show upward and downward movements. This is followed by abdominal pumping movements (HAUSL-HOFSTÄTTER, 2004). *Anthophora dalmatica* and *Odynerus melanocephalus* also show pumping movements (HAUSL-HOFSTÄTTER, 2008). During the night, the duration of resting phases increases in *Epeolus variegatus* and *Triepeolus* (no preening, no movements, the respiratory frequency decreases, and the muscle tone decreases) (KAISER, 1995).

Antenna position

In *Nomada* (*N. flava*, *Paranomada velutina*) and *Triopasites*, the antennae are directed forwards. In *Trioepolus*, however, the antennae are directed backwards, as well as in *Leiopodus singularis* and *Epeolus variegatus*. In *Eucera nigrescens*, the antennae are slightly bent backwards (PEETERS, 2012). In *Melecta obscura*, the antennae are initially directed laterally downwards; in the resting stage, the antennae are then laid out laterally on the body (HAUSL-HOFSTÄTTER, 2008). In *Anthophora dalmatica*, the antennae are also directed backwards (HAUSL-HOFSTÄTTER, 2008) as in *Amegilla q. maderae*. In *Amegilla zonata*, the antennae are directed forwards and to the side (SANDEEP & MUTHURAMAN, 2018).

Duration of falling asleep

The duration of falling asleep can be half an hour (SCHREMMER, 1955), while waking up lasts less than half an hour (15 min in *Anthophora dalmatica*, 20 and 54 min in *Melecta*; HAUSL-HOFSTÄTTER, 2008). After locking, the mouth parts are cleaned first (folding in and out of the proboscis, expelling and sucking in a drop of liquid; SCHREMMER, 1955). The trigger of resting behaviour is the onset of darkness.

Awakening process

The aggregation dissolves again in the morning. SANDEEP & MUTHURAMAN (2018) gave the time before sunrise for *Amegilla zonata*. Awakening is indicated by pumping movements and twitching of the extremities in *Anthidium septemspinosum* (HAUSL-HOFSTÄTTER, 2004). The pumping movements become increasingly faster. The antennae are raised at the end of this process (HAUSL-HOFSTÄTTER, 2004).

Only when the individuals are hit by sunlight do the mandibles detach (KAISER, 1990, 1995). They never fly away synchronously. The period of awakening until departure varied among the individuals of *A. septemspinosa* (two minutes to two hours) (HAUSL-HOFSTÄTTER, 2004). Resting phases can be switched on.

Eupavlovskia obscura begins the awakening process by raising the antennae and starting the abdominal pumping movements, stretching out the second and third pairs of legs. This is followed by tarsal movements. Finally, the antennae are fully erected again. This process can be interrupted several times by resting positions. *Melecta duodecimmaculatum* shows a similar behaviour (HAUSL-HOFSTÄTTER, 2008).

Approaches to explaining the biological background of sleeping aggregations

There are numerous explanations for the adaptive significance of sleeping aggregations (RAYMONT, 1935; GRASSÉ, 1942; EVANS & LINSLEY, 1960; EVANS & GILLASPY, 1964; FREEMAN & JOHNSTON, 1978; ALCOCK, 1998; MIYANAGA & MAETA, 1998; YOKOI *et al.*, 2017), such as primary social behaviour, thermoregulation (increase in body temperature through clustering), antipredator behaviour (increased vigilance, greater defensive behaviour, dilution effect against predators), and weather protection:

- Primary social behaviour:

Aggregations are generally not regarded as a precursor of social behavior (GRASSÉ, 1942) anymore, and this explanation is no longer mentioned in recent publications. It was based on initial observations that sleeping aggregations occurred only in solitary bee species. Later, however, such behaviour was also found in social bee species.

- Thermoregulation:

RAYMONT (1935) hypothesized that aggregations could have thermoregulatory significance. The mostly limited contact of single individuals with each other, however, speaks against thermoregulation. Nevertheless, a noticeable temperature increase in bee clusters is possible (LINSLEY & CAZIER, 1972).

- Antipredator behaviour:

LINSLEY & CAZIER (1972) studied male aggregations of *Protaxaea gloriosa*. The results largely agreed with the hypothesis of antipredator behaviour. However, their extensive temperature measurements in aggregation

clusters showed that the bees can release heat under certain conditions (*e.g.*, disturbance), resulting in a noticeable temperature increase in a cluster in a short time (in one minute, the temperature in a cluster can increase by several degrees Celsius). This could lead to the return of higher activity in the specimens, allowing them to escape predators. ALCOCK (1998) detected that the reduviid *Apiomerus flaviventris*, which visits roosting sites to find a mate, grabs and eats individual bees. If one bee is attacked, the other bees do not react. Even the presence of the bug does not cause a reaction. Occasionally, a bee may escape. Another example concerns stingless bees. Parasitic flies stay near the roosting sites of the bees and rest on the branches. In *Amegilla quadrifasciata*, phorids occur as parasites, which are also an important mortality factor in stingless male bees (SIMÕES *et al.*, 1980; BROWN, 1997). Tachinidae (*Ectophasia crassipennis*, *Tabanus sulcifrons*) are found at roosting sites of wild bees (HINE, 1906; SCHREMMER, 1955). Asilidae, too, have been observed at roosting sites (*Mallophora faultrix* near aggregations of *Nomia foxii* and *N. tetrazonata*; *Blepharepium secabilis* near those of *Protaxaea*) (EVANS & LINSLEY, 1960; LINSLEY, 1960). Crab spiders (Thomisidae) are also possible predators (RAU & RAU, 1916).

The fact that many bee individuals are present and that the predators have only a very limited influence on such large aggregations argues for a dilution effect ('selfish-herd' mechanism) (VINE, 1971). The larger the prey group, the less likely a single specimen will be captured by a predator (HAMILTON, 1971; ALCOCK, 1998; FINKBEINER *et al.*, 2012). VINE (1971) characterized this phenomenon as a 'confusion effect', and VULINEC (1990) as 'collective security'. Mixed aggregations, too, offer a protective effect analogous to the warning calls of different bird species (MAGRATH *et al.*, 2007). A high adaptive value is offered by clumped (dense) aggregations at the ends of twigs, branchlets, or culms, by linear arrangements, by diffuse (loose) aggregations, or by single individuals sitting at different locations on a plant. HAUSL-HOFSTÄTTER (2004, 2008) interpreted this behaviour as optical protection (camouflage effect) by mimicking, *e.g.*, seeds or buds. However, the exposed position also protects against nocturnal soil predators (WESTRICH *et al.*, 1992). A similar phenomenon is found in geometrid caterpillars, which are locked only by the anal feet, with the body extended horizontally, mimicking dead twigs (BARTH, 1937; SCHREMMER, 1955). FIEBRIG (1912) named such specimens 'sleep mimics'.

Sleeping aggregations in other taxonomical groups of insects: examples

Sleeping aggregations are found preferably in wild bees (Anthophoridae, Apidae, Halictidae, Megachilidae) and wasps (Chrysididae, Crabronidae, Ichneumonidae, Scoliidae, Sphecidae, Vespidae). They all show characteristic resting behaviour at night (FRISCH, 1918; BISCHOFF, 1927; GRASSÉ, 1942; EVANS & LINSLEY, 1960; LINSLEY, 1962; DAFNI *et al.*, 1981; WESTRICH, 1990; KAZENAS & TOBIAS, 1993; O'NEILL, 2001; KLEIN, 2003; WCISLO, 2003). Such behaviour is also found in numerous other insect groups:

- **Diptera:** Asilidae (FIEBRIG, 1912; RAU & RAU, 1916; HAUFE, 1962), Culicidae (FIEBRIG, 1912), Bombyliidae (RAU & RAU, 1916), Diopsidae (BURKHARDT & MOTTE, 1983; MOTTE & BURKHARDT, 1983; WILKINSON & REILLO, 1994), Drosophilidae (HENDRICKS *et al.*, 2000, SHAW *et al.*, 2000, GREENSPAN *et al.*, 2001), Tabanidae (HINE, 1906).
- **Lepidoptera:** SCHROTTKY (1908, 1922), FIEBRIG (1912), GRASSÉ (1942), MALLETT (1986), WALLER & GILBERT (1982), FINKBEINER *et al.* (2012); Pieridae (LONGSTAFF, 1906; RAU & RAU, 1916), Danaidae (SCHWARZ, 1896), Heliconiidae (SCHROTTKY, 1922; WALLER *et al.*, 1982), Noctuidae (PITTIONI, 1933), Pyralidae (ANDERSEN, 1968), Nymphalidae (RAU & RAU, 1916), Hesperidae (LONGSTAFF, 1906; RAU & RAU, 1916), Erebidae (RAU & RAU, 1916), Sphingidae (RAU & RAU, 1916), Geometridae (RAU & RAU, 1916), Lycaenidae (LONGSTAFF, 1906; FROHAWK, 1914; HERING, 1926; SCHREMMER, 1955; A. K., personal observation).
- **Coleoptera:** PEARSON & ANDERSON (1985); Cetoniidae (FIEBRIG, 1912), Cerambycidae (FIEBRIG, 1912), Coccinellidae (COPP, 1983), Rhipiphoridae (FIEBRIG, 1912), Rhynchophora (FIEBRIG, 1912), Meloidae (RAU & RAU, 1916).
- **Odonata:** RAU & RAU (1916), GRASSÉ (1942), SCHREMMER (1955), CARAYON (1967), CORBET (1999).
- **Hemiptera:** HERING (1926), CARAYON (1967).
- **Blattodea:** TOBLER (1983), TOBLER & NEUNER-JEHLE (1992), STEPHENSON *et al.* (2007).
- **Rhynchota:** FIEBRIG (1912).
- **Phasmida:** FIEBRIG (1912).
- **Orthoptera:** RAU & RAU (1916), SCHUPPE & BURROWS (1998).

CONCLUSIONS

It can be assumed that most hymenopterans show distinct sleeping behaviour. According to current knowledge, this behaviour is species-specific and shows an extraordinarily large diversity. Only a few species have been studied in detail so far. Single observations dominate, and comprehensive synoptic overviews are lacking.

The phenomenon of sleep can be defined by certain behavioural-biological features. The specimens are motionless and remain in an atypical posture compared to their usual behaviour. They are largely insensitive to external stimuli and react only to particularly strong disturbances; after the disturbance has terminated, they return to their sleeping posture (RAU & RAU, 1916). Specimens exhibit sleep homeostasis, with sleep behaviour setting in as a compensatory process within certain physiological limits depending on the extent of wakefulness (HELFRICH-FÖRSTER, 2018). It must be assumed that all organisms probably have a need for sleep to ensure homeostasis.

Roosting behaviour (branch orientation; head, leg, and antennal posture; behaviour when disturbed; abdominal pumping movements) has been studied by KAISER (1988, 1995) and others. Posture is often species- or genus-specific and apparently genetically determined, with specimens reducing the respiratory rate, releasing some muscle tension, and exhibiting a characteristic antennal posture. This has also been demonstrated by SCHULZE (1924) in the braconid *Habrobracon* and by ANDERSEN (1968) in the moth *Ephestia kuehniella* (Pyralidae). In general, sleeping individuals show a lower reaction to external stimuli (*e.g.*, in representatives of the genus *Lasioglossum*; SCHREMMER, 1955). The individual bee species differ in their resting positions, which was already pointed out by FIEBRIG (1912).

Sleep behaviour in honeybees has been studied extensively (KAISER & STEINER-KAISER, 1983; KAISER, 1988; SCHUPPE, 1995; SCHMOLZ *et al.*, 2002; SAUER *et al.*, 2003, 2004; EBAN-ROTHSCHILD & BLOCH, 2008; KLEIN *et al.*, 2008, 2010; HUSSAINI *et al.*, 2009; HARTSE, 2010; KLEIN & SEELEY, 2011; BEYAERT *et al.*, 2012; KAISER *et al.*, 2013). The most extensive genetic and neurophysiological data are available on the sleep behaviour of *Drosophila melanogaster* (HENDRICKS *et al.*, 2000; SHAW *et al.*, 2000; GREENSPAN *et al.*, 2001; CIARELLI *et al.*, 2005; BUSHEY *et al.*, 2007, 2011; SEUGNET *et al.*, 2008, 2011; DONLEA *et al.* 2011; DISSEL *et al.*, 2015; HELFRICH-FÖRSTER, 2018). For most other insect taxa, however, the knowledge of sleep behaviour is grossly incomplete. It will therefore be worthwhile to devote more attention to insect sleep behaviour in the future.

REFERENCES

- AGUIAR, C. M. L. & M. C. GAGLIANONE:
2003. Nesting biology of *Centris (Centris) aenea* (Hymenoptera, Apidae, Centridini). *Revista Brasileira de Zoologia*, **20**: 601-606.
- ALCOCK, J.:
1998. Sleeping aggregations of the bee *Idiomelissodes duplocincta* (Cockerell) (Hymenoptera: Anthophorini) and their possible function. *Journal of the Kansas Entomological Society*, **71**: 74-84.
- ALFORD, D. V.:
1975. *Bumblebees*. Davis- Poynter, London, 352 pp.
- ALDINI, R. N.:
1994. Preliminary observations on gregarious sleeping in *Amegilla* (s. str.) *garrula* (Rossi) (Hymenoptera Apoidea Anthophoridae). *Ethology, Ecology and Evolution*, **6** (sup. 1): 131-135.
- ALFKEN, J. D.:
1940. Die Arthropodenfauna von Madeira nach den Ergebnissen der Reise von Prof. Dr. O. Lundblad Juli-August 1935. XXV. Hymenoptera: Vespidae und Apidae. *Arkiv för zoologi* (Uppsala), **32** (3): 1-4.
- ALVES-dos-SANTOS, I.:
1999. Aspectos morfológicos e comportamentais dos machos de *Ancylloscelis Latreille* (Anthophoridae, Apoidea). *Revista Brasileira de Zoologia*, **16**: 37-43.
- ALVES-dos-SANTOS, I., G. A. R. MELO & J. G. ROZEN:
2002. Biology and immature stages of the bee tribe Tetrapediini (Hymenoptera: Apidae). *American Museum Novitates*, **3377**: 1-45.
- ALVES-dos-SANTOS, I., M. C. GAGLIANONE, S. R. C. NAXARA & M. S. ENGEL:
2009. Male sleeping aggregations of solitary oil-collecting bees in Brazil (Centridini, Tapinotaspidini, and Tetrapediini; Hymenoptera: Apidae). *Genetics and Molecular Research*, **8**: 515-524.
- AMIET, F. & V. MAUSS:
2003. First report of male sleeping aggregations in the pollen wasp *Celonites abbreviatus* (Villers, 1789) (Hymenoptera: Vespidae: Masarinae). *Journal of Hymenoptera Research*, **12** (2): 355-357.
- ANDERSEN, F. O.:
1968. Sleep in moths and its dependence on the frequency of stimulation in *Anagasta kuehniella*. *Opuscula Entomologica*, **33**: 15-24.
- AZEVEDO, A. A. & L. R. R. FARIA:
2007. Nests of *Phacellodomus rufifrons* (Wied, 1821) (Aves: Furnariidae) as sleeping shelter for a solitary bee species (Apidae: Centridini) in southeastern Brazil. *Lundiana*, **8**: 53-55.
- BANKS, N.:
1902. Sleeping habits of certain Hymenoptera. *Journal of the New York Entomological Society*, **10** (4): 209-214.
1908. Sleeping habit of a bee. *Entomological news, and Proceedings of the Entomological Section of the Academy of Natural Sciences of Philadelphia*, **19**: 340.
- BARTH, R.:
1937. Muskulatur und Bewegungsart der Raupen, zugleich ein Beitrag zur Spannbewegung der Spannerraupe. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, **62**: 507-566.
- BEYAERT, L., U. GREGGERS & R. MENZEL:
2012. Honeybees consolidate navigation memory during sleep. *Journal of Experimental Biology*, **215**: 3981-3988.
- BIERI, S.:
2002. Die Bienen und Wespen des Fürstentums Liechtenstein. *Naturkundliche Forschung im Fürstentum Liechtenstein*, **19**: 7-160.
- BISCHOFF, H.:
1927. *Biologie der Hymenopteren*. Julius Springer, Berlin, 598 pp.
- BLÖSCH, M.:
2000. Die Grabwespen Deutschlands. Lebensweise, Verhalten, Verbreitung. *Die Tierwelt Deutschlands*, **71**: 480 pp.
2006. 'Schlafgewohnheiten' von Wildbienen und Grabwespen (Hym.: Apidae, Sphecidae). *Galathea*, **22**: 55-66.
- BRADLEY, J. C.:
1908. A case of gregarious sleeping habits Aculeate Hymenoptera. *Annals of the Entomological Society of America*, **1**: 127-130.
- BRAUNS, H.:
1911. Biologisches über südafrikanische Hymenopteren. *Zeitschrift für wissenschaftliche Insektenbiologie*, **7**: 90-92.
- BROWN, B. V.:
1997. Parasitic phorid flies: a previously unrecognized cost to aggregation behavior of male stingless bees. *Biotropica*, **29**: 370-372.
- BRUES, C. T.:
1903. On the sleeping habits of some aculeate Hymenoptera, *Journal of the New York Entomological Society*, **11**: 228-230.
- BUDDENBROCK, W. V.:
1939. *Grundriß der vergleichenden Physiologie*. Verlag Gebrüder Borntraeger, Berlin, 1228 pp.
- BURKHARDT, D. & I. de la MOTTE:
1983. Stielaugenfliegen. *Biologie in unserer Zeit*, **13**: 92-103.
- BUSHEY, D., R. HUBER, G. TONONI & C. CIRELLI:
2007. *Drosophila* hyperkinetic mutants have reduced sleep and impaired memory. *Journal of Neuroscience*, **27**: 5384-5393.
- BUSHEY, D., G. TONONI & C. CIRELLI:
2011. Sleep and synaptic homeostasis: structural evidence in *Drosophila*. *Science*, **332**: 1576-1581.

- BUTTEL-REEPEN, H. V.:
1915. *Leben und Wesen der Bienen*. Friedrich Vieweg & Sohn, Braunschweig, 300 pp.
- CARAYON, J.:
1967. Un "dortoir" d'Hymenopteres en Provence. *Annales de la Société entomologique de France (N.S.)*, **3**: 743-755.
- CARRÉ, S. & J. P. PY:
1981. *Coelioxys rufocaudata* SM. (Hymenoptera Megachilidae) cleptoparasite de *Megachile rotundata* F. (Hymenoptera Megachilidae) pollinisateur de la luzerne. *Apidologie*, **12** (4): 303-317.
- CIRELLI, C., D. BUSHEY, S. HILL, R. HUBER, R. KREBER, B. GANETZKY & G. TONONI:
2005. Reduced sleep in *Drosophila* Shaker mutants. *Nature*, **434**: 1087-1092.
- COPP, N. H.:
1983. Temperature-dependent behaviours and cluster formation by aggregating ladybird beetles. *Animal Behaviour*, **31**: 424-430.
- CORBET, P. S.:
1999. *Dragonflies: behavior and ecology of Odonata*. Harley Books, Colchester, 829 pp.
- CRESSON, E. T.:
1865. On the Hymenoptera of Cuba. *Proceedings of the Entomological Society of Philadelphia*, **4** (1): 1-200.
1872. Hymenoptera Texana. *Transactions of the American Entomological Society*, **4**: 201.
- DAFNI, A., Y. IVRI & N. B. M. BRANTJES:
1981. Pollination of *Serapias vomeracea* Briq. (Orchidaceae) by imitation of holes for sleeping solitary male bees (Hymenoptera). *Acta Botanica Neerlandica*, **30**: 69-73.
- DEEGENER, P.:
1918. *Die Formen der Vergesellschaftung im Tierreich*. Verlag Veit, Leipzig, 420 pp.
- DISSEL, S., V. ANGADI, L. KIRSZENBLAT, Y. SUZUKI, J. DONLEA, M. KLOSE, Z. KOCH, D. ENGLISH, R. WINSKY-SOMMERER, B. van SWINDEREN & P. J. SHAW:
2015. Sleep restores behavioral plasticity to *Drosophila* mutants. *Current Biology*, **25**: 1270-1281.
- DONLEA, J. M., M. S. THIMGAN, L. SUZUKI, L. GOTTSCHALK & P. J. SHAW:
2011. Inducing sleep by remote control facilitates memory consolidation in *Drosophila*. *Science*, **332**: 1571-1576.
- DOURS, J. A.:
1869. Monographie iconographique du genre *Anthophora* Latr. *Mémoires de la Société Linnéenne du Nord de la France*, 1-211.
- EBAN-ROTHSCHILD, A. D. & G. BLOCH:
2008. Differences in the sleep architecture of forager and young honeybees (*Apis mellifera*). *Journal of Experimental Biology*, **211**: 2408-2416.
- EVANS, H. E.:
1955. An ethological study of the digger wasp *Bembecinus neglectus*, with a review of the ethology of the genus. *Behaviour*, **7**: 287-303.
1966. *The Comparative Ethology and Evolution of the Sand Wasps*. Harvard University Press, Cambridge, MA., 536 pp.
- EVANS, H. E. & E. G. LINSLEY:
1960. Notes on the sleeping aggregation of solitary bees and wasps. *Bulletin of the Southern California Academy of Sciences*, **59**: 30-37.
- EVANS, H. E. & J. E. GILLASPY:
1964. Observations on the ethology of digger wasps of the genus *Steniola* (Hymenoptera: Sphecidae: Bembicini). *The American Midland Naturalist*, **72**: 257-280.
- FABRE, J. H.:
1879. *Souvenirs entomologiques*. **1**. Libraire Delgrave, Paris, 324 pp.
1897. *Souvenirs entomologiques*. **5**. Libraire Delgrave, Paris: 349-350.
- FIEBRIG, K.:
1912. Schlafende Insekten. *Jenaische Zeitschrift für Naturwissenschaft*, **48**: 315-364.
- FINKBEINER, S. D., A. D. BRISCOE & R. D. REED:
2012. The benefit of being a social butterfly: communal roosting deters predation. *Proceedings of the Royal Society of London B*, **279**: 2769-2776.
- FREEMAN, B. E. & N. JOHNSTON:
1978. Gregarious roosting in the sphecid wasp *Sceliphron assimile*. *Annals of the Entomological Society of America*, **71**: 435-438.
- FRIESE, H.:
1888. Die Schmarotzerbienen und ihre Wirte. *Zoologische Jahrbücher Abteilung für Systematik, Geographie und Biologie der Tiere*, **3**: 847-870.
1891. Beiträge zur Biologie der solitären Blumenwespen (Apidae). *Jahrbücher Abteilung für Systematik, Geographie und Biologie der Tiere*, **5**: 751-860.
1899. Monographie der Bienengattungen *Exomalopsis*, *Ptilothrix*, *Melitoma* und *Tetrapedia*. *Annalen des Naturhistorischen Museums in Wien*, **14**: 275-276.
1908. *Die Apidae (Blumenwespen) von Argentina: nach den Reisergebnissen der Herren A. C. Jensen-Haarup und P. Jörgensen in den Jahren 1904-1907*. Verlag Flora og Fauna, 111 pp.
1923. *Die europäischen Bienen (Apidae). Das Leben und Wirken unserer Blumenwespen*. Walter de Gruyter, Berlin & Leipzig, 456 pp.
- FRISCH, K. V.:
1918. Beitrag zur Kenntnis sozialer Instinkte bei solitären Bienen. *Biologisches Zentralblatt*, **38**: 183-188.
- FROHAWK, F. W.:
1914. The sleeping attitude of Lycaenidae. *Entomologist*, **47**: 212-213.

- GEISER F.:
1988. *Wildbienen – Wehrhafte Blumenkinder*. Landbuch Verlag, Hannover, 135 pp.
- GILLASPY, J. E.:
1963. The genus *Stizoides* (Hymenoptera: Sphecidae: Stizini) in North America, with notes on the Old World fauna. *Bulletin of the Museum of Comparative Zoology at Harvard College*, **128**: 371-391.
- GILLASPY, J. E., H. E. EVANS & C. S. LIN:
1962. Observations on the behavior of digger wasps of the genus *Stictiella* (Hymenoptera: Sphecidae) with a partition of the genus. *Annals of the Entomological Society of America*, **55**: 559-566.
- GOTTSBERGER, G., J. M. F. CAMARGO & I. SILBERBAUER-GOTTSBERGER:
1988. A bee-pollinated tropical community: The beach dune vegetation of Ilha de São Luís, Maranhão, Brazil. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, **109**: 469-500.
- GRANDI, G.:
1961. Studi di un entomologo sugli imenotteri superiori. *Bolletino dell'Istituto di Entomologia dell'Universita di Bologna*, **25**: 1-19.
- GRASSÉ, P.-P.
1942. Les rassemblements de sommeil des Hyménoptères et leur interprétation. *Bulletin de la Société Entomologique de France*, **47**: 142-148.
- GREENSPAN, R. J., G. TONONI, C. CIRELLI & P. J. SHAW:
2001. Sleep and the fruit fly. *Trends in Neurosciences*, **24**: 142-145.
- GUEINZIUS, M.:
1858. On the habits of the Hymenoptera of Natal. *Zoologist*, **1858**: 6037-6039.
- HAMILTON, W. D.:
1971. Geometry for the Selfish Herd. *Journal of Theoretical Biology*, **31**: 295-311.
- HARTSE, K. M.:
2010. Sleep in insects. In: *Evolution of sleep: phylogenetic and functional perspectives* (ed.: S. T. Harbison): 34-56.
- HAUFE W. O.:
1962. Ethological and statistical aspects of a quantal response in mosquitoes to environmental stimuli. *Behaviour*, **20**: 221-241.
- HAUSL-HOFSTÄTTER, U.:
2004. Beobachtungen an einer Nachtruhegemeinschaft der Wollbiene *Anthidium septemspinus* Lepeletier 1841 (Hymenoptera, Apoidea, Megachilidae). *Linzer biologische Beiträge*, **36** (2): 801-822.
2008. Beobachtungen an nachtruhenden Hymenopteren in der Umgebung von Mali Lošinj, Kroatien (Anthophoridae, Andrenidae, Eumenidae, Scoliidae, Ichneumonidae). *Joannea Zoologie*, **10**: 101-121.
- HELFRICH-FÖRSTER, C.:
2018. Sleep in insects. *Annual Review of Entomology*, **63**: 69-86.
- HENDRICKS, J. C., S. M. FINN, K. A. PANCKERI, J. CHAVKIN, J. A. WILLIAMS, A. SEHGAL & A. I. PACK:
2000. Rest in *Drosophila* is a sleep-like state. *Neuron*, **25** (1): 129-138.
- HERING, M.:
1926. *Biologie der Schmetterlinge*. Biologische Studienbücher III. Julius Springer Verlag, Berlin, 516 pp.
- HILL, R.:
1865. Zoology: The sleep of insects. In: *Annual of Scientific Discovery: Year Book of Facts and Science and Art for 1864*. (ed.: D. A. Wells): 278-282.
- HINE, J. S.:
1906. Habits and life histories of some flies of the family Tabanidae. *Technical series / Bureau of Entomology United States Department of Agriculture*, **12**: 19.
- HUSSAINI, S. A., L. BOGUSCH, T. LANDGRAF & R. MENZEL:
2009. Sleep deprivation affects extinction but not acquisition memory in honey-bees. *Learning & Memory*, **16**: 698-705.
- JOSEPH, H. C.:
1929. Le repos nocturne chez quelques Hyménoptères du Chili. *Zoologischer Anzeiger*, **82**: 414-421.
- KAISER, W.
1988. Busy bees need rest, too. Behavioural and electromyographical sleep signs in honeybees. *Journal of Comparative Physiology A*, **163**: 565-584.
1990. Wie solitäre Bienen die Nacht verbringen. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **83**: 616-617.
1995. Rest at night in some solitary bees – a comparison with the sleep-like state of honey bees. *Apidologie*, **26** (3): 213-230.
- KAISER, W. & J. STEINER-KAISER:
1983. Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature*, **301**: 707-709.
- KAISER, W., T. WEBER, D. OTTO & A. MIROSCHNIKOW:
2013. Oxygen supply of the heart and electrocardiogram potentials with reversed polarity in sleeping and resting honey bees. *Apidologie*, **45**: 73-87.
- KAZENAS, V. L. & V. I. TOBIAS:
1993. Night-sleeping aggregations of digger wasps (Hymenoptera, Sphecidae) in Southeastern Kazakhstan. *Entomological Review*, **71**: 13-16.
- KEARLEY, G.
1857. On the habit of *Chelostoma florissomnis*. *Zoologist*, **1857**: 5770.
- KLEIN, B. A.:
2003. Signatures of sleep in a paper wasp. *Sleep*, **26**: A115-A116.
- KLEIN, B. A. & T. D. SEELEY:
2011. Work or sleep? Honeybee foragers opportunistically nap during the day when forage is not available. *Animal Behaviour*, **82**: 77-83.

- KLEIN, B. A., K. M. OLZSOWY, A. KLEIN, K. M. SAUNDERS & T. D. SEELEY:
2008. Caste-dependent sleep of worker honey bees. *Journal of Experimental Biology*, **211**: 3028-3040.
- KLEIN, B. A., A. KLEIN, M. K. WRAY, U. G. MUELLER & T. D. SEELEY:
2010. Sleep deprivation impairs precision of waggle dance signaling in honey bees. *Proceedings of the National Academy of Sciences*, **107** (52): 22705-22709.
- KRATOCHWIL, A., J. SMIT & A. AGUIAR:
2018. Updated checklist of the wild bees of the Madeira Archipelago (Hymenoptera: Apoidea: Anthophila). *Linzer biologische Beiträge*, **50** (2): 1213-1228.
- KRATOCHWIL, A., A. SCHWABE, A. M. F. AGUIAR & J. SMIT:
2022. Intra-island distribution of the wild-bee species of Madeira Island, habitat preferences and flower-visiting behaviour (Hymenoptera, Apoidea, Anthophila). *Boletim do Museu de História Natural do Funchal*, **22** (366): 55-113.
- LANDES, D. A. & J. H. HUNT:
1988. Occurrence of *Chalybion zimmermanni zimmermanni* Dahlbom in a mixed sleeping aggregation with *Chalybion californicum* (Saussure) in Missouri (Hymenoptera: Sphecidae). *Journal of the Kansas Entomological Society*, **61**: 230-231.
- LIEFTINCK, M. A.:
1956. Revision of some oriental Anthophorine bees of the genus *Amegilla* Friese (Hymenoptera, Apoidea). *Zoologische Verhandlungen*, **30**: 1-41.
1957. De slobkousbij en haar gewooten. *De Levend Natuur*, **60**: 121-128.
1958. A preliminary account of the bees of the Canary Islands (Hym., Apoidea). *Societas Scientiarum Fennica, Commentationes Biologica*, **18** (5): 1-34.
- LINNAEUS, C.:
1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. – Vindobonæ [Vienna], Typis Ioannis Thomæ, 1-824.
- LINSLEY, E. G.:
1958. The ecology of solitary bees. *Hilgardia*, **27**: 543-599.
1960. Ethology of some bee – and wasp-killing robber flies of Southeastern Arizona and Western New Mexico. *University of California Publications in Entomology*, **16**: 357-392.
1962. Sleeping aggregations of solitary Hymenoptera II. *Annals of the Entomological Society of America*, **55**: 148-164.
- LINSLEY, E. G. & MCSWAIN, J. W.:
1958. Sleeping habits of males of *Hesperapis* (Hymenoptera: Mellitidae). *Journal of the Kansas Entomological Society*, **28**: 273-274.
- LINSLEY, E. G. & M. A. CAZIER:
1972. Diurnal and seasonal behavior patterns among adults of *Protoxaea gloriosa* (Hymenoptera, Oxaeidae). *American Museum Novitates*, **2509**: 1-25.
- LONGSTAFF, G. B.:
1906. Some rest-attitudes of butterflies. *Transactions of the Royal Entomological Society of London*, **42**: 97-118.
- LÜDERWALDT, H.:
1910. Zur Biologie zweier brasilianischer Bienen. *Zeitschrift für wissenschaftliche Insektenbiologie*, **6**: 297-298.
- MAGRATH, R. D., B. J. PITCHER & J. L. GARDNER:
2007. A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology*, **18** (5): 944-951.
- MAHLMANN, T., J. HIPÓLITO & F. F. OLIVEIRA:
2014. Male sleeping aggregation of multiple Eucerini bee genera (Hymenoptera: Apidae) in Chapada Diamantina, Bahia, Brazil. *Biodiversity Data Journal*, **2** (2): 15-56.
- MALLET, J.:
1986. Gregarious roosting and home range in *Heliconius* butterflies. *National Geographic Research*, **2**: 198-215.
- MARTINS, H., P. REBOUÇAS & V. FERREIRA:
2018. Sleeping aggregation of an oil-collecting bee, *Centris (Paracentris) xanthomelaena* Moure & Castro (Hymenoptera: Apidae: Centridini). *Sociobiology*, **65** (4), 770-772.
- MATHEWSON, J. A. & H. V. DALY:
1955. A brief note on the sleep of male *Melissodes* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society*, **28**: 120.
- MIYANAGA R. & Y. MAETA:
1998. Notes on a male sleeping aggregation of *Lasioglossum (Ctenonomia) kumejimense* (Hymenoptera: Halictidae). *Entomological Science*, **1** (3): 357-358.
- MIYANAGA, R., Y. MAETA & M. D. A. HANNAN:
2011. Notes on the nesting biology of *Amegilla florea urens* (Cockerell) in Iriomote Island, Southernmost archipelago of Japan (Hymenoptera, Apidae). *New Entomologist*, **60**: 35-44.
- MOTTE, I. de la & D. BURKHARDT:
1983. Portrait of an asian stalk-eyed fly. *Naturwissenschaften*, **70**: 451-461.
- MÜLLER, A.:
1991. Wildbienen im Schaffhauser Randen. *Neujahrsblatt der Naturforschenden Gesellschaft Schaffhausen*, **43**: 1-78.
- MÜLLER, A., A. KREBS & F. AMIET:
1997. *Bienen: Beobachtung, Lebensweise*. Naturbuch-Verlag, München, 384 pp.
- NEWMAN, E.:
1859. Bees roosting by the mandibular process. *The Zoologist*, **1859**: 6468.

- OLIVEIRA, F. F. & M. S. CASTRO:
2002. Nota sobre o comportamento de agregação de machos de *Oxaea austera* Gerstaecker (Hymenoptera, Apoidea, Oxaeinae) na Caatinga do Estado da Bahia, Brasil. *Revista Brasileira de Zoologia*, **19**: 301-303.
- O'NEILL, K. M.:
2001. *Solitary Wasps*. Cornell University Press, Ithaca, New York, 406 pp.
- PEARSON, D. L., & J. J. ANDERSON:
1985. Perching heights and nocturnal communal roosts of some tiger beetles (Coleoptera: Cicindelidae) in southeastern Peru. *Biotropica*, **1985**: 126-129.
- PEETERS, T. M. J.:
2012. Sleep and sleeping aggregations of solitary bees (Apidae sl) in The Netherlands. *Entomologische Berichten*, **72** (1/2): 85-90.
- PÉREZ, J. M.:
1889. *Les abeilles*. Hachette et Cie, Paris, 375 pp.
- PITTIONI, B.:
1933. Über Schlafgesellschaften solitärer Insekten. *Verhandlungen der zoologisch-botanischen Gesellschaft in Wien*, **83**: 192-201.
- PITTIONI, B. & R. SCHMIDT:
1943. Die Bienen des südöstlichen Niederdonau II, Andrenidae und isoliert stehende Gattungen. *Natur und Kultur, Museum des Reichsgaues Niederdonau*, **24**: 1-89.
- RAJMOHANA, K., P. GIRISH KUMAR & A. MAJUMDER:
2018. Record of sleeping aggregation of the solitary aculeate potter wasp *Antepipona bipustulata* (de Saussure, 1855) (Hymenoptera: Vespidae: Eumeninae) from India. *Records of the Zoological Survey of India*, **118** (2): 212-213.
- RAU, P.:
1938. Additional observations on the sleep of insects. *Annals of the Entomological Society of America*, **31**: 540-556.
- RAU, P. & N. RAU:
1916. The sleep of insects; an ecological study. *Annals of the Entomological Society of America*, **9**: 227-274.
- RAYMENT, T.:
1935. *A cluster of bees*. Endeavour Press, Sydney, 752 pp.
- RITSEMA, C.:
1879. Naamlijst der tot heden in Nederland waargenomen bijen-soorten (Hymenoptera Anthophila). *Tijdschrift voor Entomologie*, **22**: 21-55.
- ROTH, P.:
1928. Les Ammophiles de l'Afrique du Nord. *Annales de la Société entomologique de France* (N. S.), **97**: 153-240.
- SABINO, W. O., C. I. SILVA, & I. ALVES-DOS-SANTOS:
2017. Mating system and sleeping behaviour of the male and female *Centris (Paracentris) burgdorfi* Friese. *Journal of Insect Behavior*, **30**: 103-118.
- SANDEEP, K. J. & M. MUTHURAMAN:
2018. Behavior of blue banded bees, *Amegilla zonata* L. (Apidae: Hymenoptera). *Journal of Entomology and Zoology Studies*, **6** (5): 2365-2370.
- SANTOS, C. F., C. MENEZES, A. VOLLET-NETO & V. L. IMPERATRIZ-FONSECA:
2014. Congregation sites and sleeping roost of male stingless bees (Hymenoptera: Apidae: Meliponini). *Sociobiology*, **61** (1): 115-118.
- SARAVANAN, P. A.:
2005. *Studies on certain aspects of biology, behavior and economic utility of stingless bees*. Ph.D. Thesis Tamil Nadu Agricultural University, Coimbatore, India, 117 pp.
- SASAKI, Y. & T. SASAKI:
2008. Notes on the sleeping aggregation of a sweat bee, *Halictus (Seladonia) aerarius* Smith (Hymenoptera, Halictidae). *Chugoku Kontyu*, **22**: 47-48.
- SAUER, S., M. KINKELIN, E. HERRMANN & W. KAISER:
2003. The dynamics of sleep-like behaviour in honey bees. *Journal of Comparative Physiology A*, **189**: 599-607.
- SAUER, S., E. HERRMANN & W. J. KAISER:
2004. Sleep deprivation in honey bees. *Journal of Sleep Research*, **13**: 145-152.
- SAUNDERS, E.:
1896. *The Hymenoptera Aculeata of the British Islands: a descriptive account of the families, genera, and species indigenous to Great Britain and Ireland, with notes as to habits, localities, habitats, etc.* Reeve, London, 391 pp.
- SCHEUCHL, E. & W. WILLNER:
2016. *Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt*. Quelle & Meyer Verlag, Wiebelsheim, Germany. 920 pp.
- SCHMOLZ, E., D. HOFFMEISTER & I. LAMBRECHT:
2002. Calorimetric investigations on metabolic rates and thermoregulation of sleeping honeybees (*Apis mellifera carnica*). *Thermochimica Acta*, **382**: 221-227.
- SCHREMMER, F.:
1955. Beobachtungen über die Nachtruhe bei Hymenopteren, insbesondere die Männchenschlafgesellschaften von *Halictus*. *Österreichische Zoologische Zeitschrift*, **6**: 70-89.
- SCHROTTKY, C.:
1908. Blumen und Insekten in Paraguay. *Zeitschrift für wissenschaftliche Insektenbiologie*, **4**: 22-26.
1922. Soziale Gewohnheiten bei solitären Insekten. *Zeitschrift für wissenschaftliche Insektenbiologie*, **17**: 49-57.
- SCHULZE, H.:
1924. Über die Fühlerhaltung von *Habrobracon* zugleich ein Beitrag zur Sinnesphysiologie und Psychologie dieser Schlupfwespe. *Zoologischer Anzeiger*, **61**: 122-134.
- SCHUPPE, H.:
1995. Rhythmic brain activity in sleeping bees. *Wiener Medizinische Wochenschrift*, **145**: 463-464.
- SCHUPPE, H. & M. BURROWS:
1998. Arousal shifts in quiescent locusts. *Journal of Experimental Biology*, **201**: 1719-1728.

- SCHWARZ, E. A.:
1896. Sleeping trees of Hymenoptera. *Proceedings of the Entomological Society of Washington*, **4**: 24-27.
- SEUGNET, L., L. SUZUKI, J. M. DONLEA, L. GOTTSCHALK & P. J. SHAW:
2011. Sleep deprivation during early-adult development results in long-lasting learning deficits in adult *Drosophila*. *Sleep*, **34**: 137-46.
- SEUGNET, L., L. SUZUKI, L. VINE, L. GOTTSCHALK & P. J. SHAW:
2008. D1 receptor activation in the mushroom bodies rescues sleep-loss-induced learning impairments in *Drosophila*. *Current Biology*, **18**: 1110-1117.
- SHAW, P. J., C. CIRELLI, R. J. GREENSPAN & G. TONONI:
2000. Correlates of sleep and waking in *Drosophila melanogaster*. *Science*, **287**: 1834-1837.
- SICHEL, F. J.:
1867. Hymenoptera mellifera. In: *Die Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair. Zoologischer Theil, 2. Band, I. Abtheilung, A., Hymenoptera* (ed.: H. de Salissure), Wien, Kaiserlich-Königliche Hof- und Staatsdruckerei; in Commission bei K. Gerold's Sohn, Wien, 143-156.
- SILVA, M. D. E., A. C. R. ANDRADE-SILVA & M. SILVA:
2011. Long-term male aggregations of *Euglossa melanotricha* Moure (Hymenoptera: Apidae) on fern fronds *Serpocaulon triseriale* (Pteridophyta: Polypodiaceae). *Neotropical Entomology*, **40**: 548-552.
- SIMÕES, D., L. R. BEGO, R. ZUCCHI & S. F. SAKAGAMI:
1980. *Melaloncha sinistra* Borgmeier, an endoparasitic phorid fly attacking *Nannotrigona* (*Scaptotrigona*) *postica* Latr. (Hym., Meliponinae). *Revista Brasileira de Entomologia*, **24**: 137-142.
- SNELLEN van VOLLENHOVEN, S. C.:
1858. Naamlijst van Nederlandsche Vliesvleugelige Insekten (Hymenoptera). In: *Bouwstoffen voor eene Fauna van Nederland II* (ed.: J. A. Herklots). Leiden: 221-283.
- STARR, C. K. & D. VELEZ:
2009. A dense daytime aggregation of solitary bees (Hymenoptera: Apidae: Centridini) in the Lesser Antilles. *Journal of Hymenoptera Research*, **18** (2): 175-177.
- STARR, C. K. & L. R. HERNANDEZ:
1995. A daytime resting aggregation of male *Pepsis sericans* (Pompilidae). *Sphecos*, **29**: 12-13.
- STEPHEN, W. P., G. E. BOHART & P. F. TORCHIO:
1969. *The Biology and External Morphology of Bees with a Synopsis of the Genera of North-western America*. Agricultural Experiment Station, Oregon State University. 140 pp.
- STEPHENSON, R., K. R. CHU & J. LEE:
2007. Prolonged deprivation of sleep-like rest raises metabolic rate in the Pacific beetle cockroach, *Diploptera punctata* (Eschscholtz). *Journal of Experimental Biology*, **210**: 2540-2547.
- SUGIURA, N.:
1991. Male territoriality and mating tactics in the wool-carder bee, *Anthidium septemspinum* Lapeletier (Hymenoptera, Megachilidae). *Journal of Ethology*, **9**: 95-103.
- THOENES, S. C.:
1994. Description of a sleeping aggregation of male *Chalicodoma chilopsis* (Cockerell) (Hymenoptera: Megachilidae). *The Pan-Pacific Entomologist*, **70**: 328-330.
- TOBLER, I.:
1983. Effect of forced locomotion on the rest-activity cycle of the cockroach. *Behavioural Brain Research*, **8**: 351-360.
- TOBLER, I. & M. NEUNER-JEHLE:
1992. 24-h variation of vigilance in the cockroach *Blaberus giganteus*. *Journal of Sleep Research*, **1**: 231-239.
- VERHOEFF, C.:
1892. Ueberkämpfende und gesellige Bienenmännchen. *Entomologische Nachrichten*, **18**: 244-248.
- VINE, I.:
1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, **30**: 405-422.
- VULINEC, K.:
1990. Collective security: aggregation by insects as a defense. In: *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators* (eds: D. L. Evans & J. O. Schmidt): 251-288.
- WALLER, D. A. & L. E. GILBERT:
1982. Roost recruitment and resource utilization: observations on a *Heliconius charitonia* L. roost in Mexico (Nymphalidae). *Journal of the Lepidopterists' Society*, **36**: 178-184.
- WESTWOOD, J. S.:
1840. *An Introduction to the Modern Classification of Insects: Founded on the Natural Habits and Corresponding Organisation of the Different Families*. Longman, Orme, Brown, Green, and Longmans, London, 158 pp.
- WCISLO, W. T.:
2003. A male sleeping roost of a sweat bee, *Augochlorella neglectula* (Ckll.) (Hymenoptera: Halictidae), in Panamá. *Journal of the Kansas Entomological Society*, **76**: 55-59.
- WESTRICH, P.:
1989. *Die Wildbienen Baden-Württembergs*. Eugen Ulmer Verlag, Stuttgart, 972 pp.
1990. *Die Wildbienen Baden-Württembergs*. 2. Auflage. Eugen Ulmer Verlag, Stuttgart. 972 pp.
- WESTRICH, P., L. WESTRICH & A. MÜLLER:
1992. Beobachtungen zur Nachtruhe der Kraftbiene *Blastes emarginatus* (Schenck) (Hymenoptera, Apoidea, Anthophoridae). *Linzer biologische Beiträge*, **24** (1): 3-12.
- WILKINSON, G. S. & P. R. REILLO:
1994. Female choice response to artificial selection on

an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society of London B*, **255** (1342): 1-6.

YOKOI, T. & M. WATANABE:

2014. Sharing of overnight site with *Amegilla florea urens* and *Notocrypta curvifascia curvifascia* in Iriomote Island. *Chugoku Kontyu*, **27**: 23-24.


2015. Female-biased sleeping aggregations of *Amegilla florea urens* (Hymenoptera: Apidae). *Entomological Science*, **18**: 274-277.

YOKOI, T., N. IDOGAWA, T. KONAGAYA & M. WATANABE:

2016. The non-use of sleeping substrate by the sympatric bees *Amegilla florea urens* and *A. senahai senahai* (Hymenoptera: Apoidea). *Entomological News*, **126** (2): 138-143.

YOKOI, T., N. IDOGAWA, I. KANDORI, A. NIKKESHI & M. WATANABE:

2017. The choosing of sleeping position in the overnight aggregation by the solitary bees *Amegilla florea urens* in Iriomote Island of Japan. *The Science of Nature*, **104** (3-4): 23.

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