Thermochimica Acta 361 (2000) 121–129

thermochimica acta

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Thermoanalytical investigations on paper covers of social wasps

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Received 10 January 2000; accepted 17 January 2000

Abstract

Paper nests of wasps and hornets were investigated by means of differential scanning calorimetry (DSC), thermogravimetry (TG) in combination with mass spectrometry (MS), combustion calorimetry (CC) and some other biophysical techniques. Nests are constructed of thin paper layers (0.1 mm thick, area density 76.5 g m^{-2}) formed of rotten wood and strengthened with saliva as adhesive. The nest material is water repellent with extremely low water content (about 3%). Paper nests establish a microclimate for the insect colony due to the good thermal insulation (heat conductivity 0.08–0.20 W (°C m)$^{-1}$ comparable to that of some bird nests or of good natural and technical insulators. DSC and TG thermograms show that cellulose is the main component in the wasp paper offering high tensile strength against deformation and a low specific weight for light construction and easy transport.

Keywords: Differential scanning calorimetry; Insects; Paper nests; Thermoregulation; Wasps

1. Introduction

Nest constructing abilities and activities are found in the whole animal kingdom, from insects up to vertebrates: as foam-nests for frogs, plant nests for the stickle-back fish (*Gasterosteus aculeatus*), artistically designed brood nests of the harvest-mouse (*Micromys domesticus*) or sleeping-nests for anthropoid apes, but of course best known in the connection with birds [1]. These abilities were developed during evolution to support the parents in rearing the young. All nests offer an effective insight into the life of a species and the conditions for surviving in an adverse environment. The produced nest type is a specific pecularity of a species just as behaviour, appearance, morphology or physiology. At the same time, a nest gives a somehow permanent record of the behaviour (‘frozen behaviour’) of its constructor [2]. “The primary, basic, and most general functions of a nest are to help insure warmth and safety for the developing eggs and young” [2]. Although written for the nests of birds, this statement holds also good for the insect nests of our interest.

Some insect species — among them mainly paper wasps (*Polistinae*) and other social wasps as yellow jackets and hornets (*Vespinae*), some termites and ants — construct paper covers for their nests to improve the thermoregulatory behaviour. This ability developed simultaneously with the social behaviour some 50 million years ago in the eocene period [3]. Such insects use slightly rotten, intensively chewed wood as the basic material and the secretion of their saliva glands as adhesive. Fresh wood is only taken in a few cases [3]. The binding agent of the nest material—corresponding to the glue in real paper making—is the wasps’ spittle, a chitin-like secretion from the labial

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0040-6031/00/$ – see front matter
PII: S0040-6031(00)00553-0

glands [4]. During drying it binds the wood fibres loosely together and hardens quickly and irreversibly to a water insoluble, water repellent horny substance. Supposedly this adhesive is added during the fibre collection in the field [3]. In a similar way, some bird species (e.g. swifts and swiftlets) use saliva to consolidate their nests and to attach them to vertical substrates [2]. Mucoproteins in the saliva are responsible for these glueing properties due to their ability to form rubbery gels [5]. Other types of insect nests may be produced from silk as in the Eastern Tent Caterpillar *Malacosoma americanum* and serve the same purposes of sheltering [6].

Wasp and hornet nests — similar to those of birds — also prepare a special microclimate for the brood and protect against cold, heat, drought, wind, rain and some predators. Constructed from multi-layers of paper with dead air spaces between them or with downward opened air pockets (see below) they use the effect that heat moves faster through the paper sheets than through the still air entrapped between them and gain a maximum of insulation with a minimum of material and energy input. A good thermal insulation allows the absence of workers from the nest and thus a prolonged time for foraging activities without the danger of a too strong temperature loss.

The paper nests of social insects awoke the interest of many scientists long ago. The first scientific report was given in 1719 by Rene de Réaumur to the French Academy. Numerous other observations and investigations followed. In the framework of our energetic investigations of social-insect colonies nest envelopes of different wasp species were investigated by means of thermoanalytical methods. Results of combustion calorimetry, differential scanning calorimetry (DSC), heat conduction measurements, thermogravimetry (TG) and gravimetric determinations of the different nest components were compared with those from fresh or partly rotten wood, the main constructing material of wasps. Infrared thermography on active nests clearly showed the influence of thermal insulation and the manner in which wasps proceed with the construction of their nests during the summer season. Some general remarks and data on thermal analysis of paper can be found in Section 14.12 '*Wood and Paper*' of the review of Wiedemann and Lamprecht [7].

2. Experimental and material

2.1. Nests

Wasp and hornet nests are usually hanging from a substrate. The essential difference to an artificial or natural bee-hive becomes evident in the horizontal combs with downwards opened cells made from wood. They demonstrate that cells are exclusively used for rearing the brood and never for storing organic matter as food. Fig. 1 presents a nest of the long-cheeked wasp *Dolichovespula saxonii* in an inverted position partly opened to show the construction of the envelope (see specially at the entrance) and the horizontal combs. Due to our experimental approach, this nest was directly attached to the wooden support without a pedicel. To give an impression of the real size of the nest some wasps are placed in front of it. The multilayered envelope, three horizontal combs and the entrance at the bottom are clearly

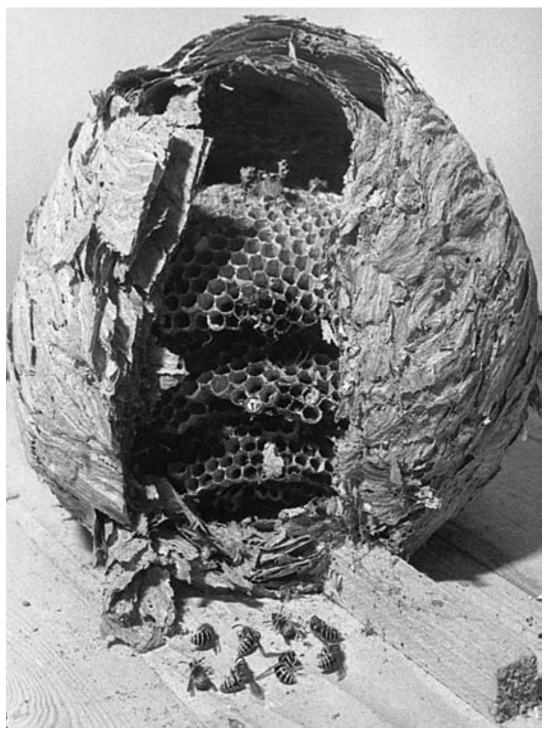

Fig. 1. Inverted nest of the long-cheeked wasp *D. saxonii*. For details see text.

indicated. The combs are connected to one another by pillars to leave sufficient space between them.

Nests used in the present investigation were collected from outside locations in Berlin at the end of the wasp season when the young inseminated queens had left for their hibernating places and the workers had died in the following days. The fragile nests were carefully transported in total to the Institute for Biophysics and kept there at room temperature and humidity till to their use. Most nests with sizes from 10 cm×10 cm to 30 cm×60 cm for a prolate spheroid originated from the common European hornet *Vespa crabro* L. and only a few from the wasp *D. saxonii*. The nests were divided in their different parts: (i) the rod-like pedicel which establishes the connection between the supporting substrate and the nest proper; (ii) the nest envelope formed of several layers of paper-like matter; (iii) the empty combs of the brood; (iv) the silk cover at some of the combs, and (v) larval faeces which are defecated before pupation and become a dark, hard matter (called meconium) at the bottom of the cells. These five parts were investigated separately. Moreover, component (ii) was subdivided according to its colour for different wood origins.

Wasps nests are constructed from thousands of small wood particles of a few milligrams from different sources. This diversity is the reason for the fascinating surface patterns found in these nests (see Fig. 1). Wasps prefer weathered or decayed wood which is easier to divide in suited small samples. Depending on the type of wood, the degree of microbial decomposition by white, brown or soft rot or the time of weathering the chemical composition may change considerably. Within 25 years 80% of the original lignin may be decomposed, 10% of the cellulose and hemicellulose changed and the ash content increased 10-fold due to dust from the air [3]. It is, thus, understandable that this paper material is extremely heterogene and that the results of chemical, biophysical or thermoanalytical investigations scatter significantly.

2.2. Thermoanalytic determinations

Most thermoanalytical investigations (DSC) were run in a differential scanning calorimeter, type DSC 910, series 99, DuPont Instruments (STA, Alzenau, Germany) with a sensitivity of 235 $\mu W\,mV^{-1}$ and sample sizes around 10 mg. The specimens were burnt in open or loosely covered pans, sometimes under a flow of nitrogen, with heating rates of 20 $K\,min^{-1}$ and a temperature range of 30–600°C.

Additional thermoanalytical (TG/DTG) experiments were performed in the same temperature range with a combination of a thermobalance (Seiko TG/DTA 220, Seiko, Karlsruhe) and a quadrupole mass spectrometer (MS) (QMG 421 C, Balzers, Wiesbaden, Germany) with nitrogen as purge gas, sample sizes of about 3 mg and heating rates of 10 $K\,min^{-1}$.

2.3. Combustion calorimetry

Combustion heats were determined with a modified Phillipson bomb calorimeter calibrated with benzoic acid (26.436 $kJ\,g^{-1}$, Riedel-deHaen AG, Seelze, Germany) [8]. Sample sizes ranged from 10 to 30 mg DW (dry weight), the oxygen pressure was set to 2.5 MPa, the sensitivity amounted to 86 $J\,mV^{-1}$. If possible, samples were pressed to pills, otherwise burnt in gelatine capsules (combustion heat 19.6 $kJ\,g^{-1}$). Ignition was initiated by discharging a 5000 μF capacitor via a nickeline fuse wire of 0.1 mm diameter.

2.4. Heat conductivity

At the end of the season empty hornet nests were equipped with electrical heaters of 10 Ω and electrical powers of up to 10 W. The internal temperature of the nest as function of the ambient temperature and the heating power rendered a linear slope from which the heat conductivity could be calculated [9,10].

2.5. Additional characteristic data of nests

The water content of the different parts of nests was determined by specimen drying in a desiccator at 105°C till weight constancy, usually for 24 h. Ash contents were obtained from the remaining weights in DSC and TG experiments, but with higher accuracy from separate ashing of samples with several grams in titanium crucibels on a Bunsen burner or in a muffel furnace (type MES02 with two step controller Tempat, Messner, Dettenhausen, Germany) at 550°C for 6 h. For an appropriate choice of the experimental parameters see [11].

2.6. Infrared photography (thermography)

Surface temperatures of an active hornet nest were determined by means of an infrared-thermography camera (Zeiss Heotherm-SK, Zeiss, Oberkochem, Germany) connected to a monitor (Trinitron PVM-1443MD, Sony, Köln, Germany), a plotter (type 4692, Tektronix, Köln, Germany) and a computer with video interface (Gama Data, Hewlett-Packard, Böblingen, Germany). The room temperature was set to 18°C. The system was installed in the Radiation Department of the University Clinicum Rudolf Virchow of the Free University, Berlin.

3. Results and discussion

3.1. Construction of the envelope

The envelopes of wasp nests are constructed of several thin layers of a paper-like matter and show additionally downwards opened pockets in which the ascending warm air is collected. This makes it difficult to give the exact wall size of the envelope and a correct number of layers for a specific nest. Several colonies of hornets were reared artificially in wooden boxes equipped with electric heaters. The hope was that the hornets would renounce the envelope and just concentrate on the construction of combs, thus facilitating the experimental observation of the colony life. But also under these conditions at least an envelope of one layer was produced.

An individual layer of the envelope has an areal density of 76.5 g m^{-2} at a mean thickness of 0.1 mm. Both values together lead to a specific mass density in the layers of about 800 kg m^{-3}, corresponding to that of dry wood (400–800 kg m^{-3}). The areal density of 76.5 g m^{-2} equals that of usual writing-paper (80–110 g m^{-2}). Due to the multiple layers and the additional air pockets at the surface up to 2.7 m^2 of envelope material are used to construct a large nest. McGovern et al. found values of 0.114 mm and 43.4 g m^{-2} for a *Vespula* nest [3] confirming our own observations.

The envelopes hanging from the supporting substrate by means of the pedicel have their entrance always at the bottom — even when they are constructed in experimental boxes with an exit to the ambient surroundings at the side. In this way, they resemble the nests of many weaver birds which use the same construction for a better protection of their brood [2]. Moreover, the first comb level may be abandoned during development of the wasp nest and connected to the envelope. Thus, the internal volume is reduced leading to an increased insulation at the top, a reduced active surface and a concentration of animal activity in the centre [9].

For a realistic appreciation of the energetic significance of the wasp nest it is necessary to compare the energy input into its construction with the energy gain for the colony. This may be done in the following rough estimation: the mean mass of a piece of wood pulp collected by a hornet during a typical foraging flight of 15 min amounts to 7.6 mg and corresponds to a layer of 1 cm^2. A hornet nest envelope of 23 g would thus consume about 3000 particles and 750 foraging hours. A hornet worker flies at a power of about 72 mW at a mean ambient temperature of 20°C [12], so that the total foraging hours are equivalent to $750\times72=54{,}000$ mWh or 194 kJ. Such an amount of energy is equivalent to 5 days of heating the nest during normal summer days and is thus negligible in the total energy balance.

It was shown by Singer and Espelie [13] that specific long-chain hydrocarbons are not only present on cuticles of adult wasps (*Polistes metricus* Say) or on larvae and eggs, but also on the nest and the pedicel surface. The authors could show that the effect of these hydrocarbons which are supposed to be responsible for the nestmate recognition is maximal in contact with the nest and not with the insects and that these substances may play a defensive role at the pedicel. At the same time one can speculate that these hydrocarbons provide the same hydrophobic barrier for the pedicel and the nest as they do on the cuticle of the insects protecting them from desiccation.

3.2. Thermal conductivity

An important factor for the proper insulation of the hornet nest is the thermal conductivity of the whole envelope. The heating up of empty nests at the end of the wasp season by an electric resistance and a known electric power rendered constant temperature regimes at constant ambient temperature *T*. Fig. 2 exhibits the linear relationship between the heating power and the

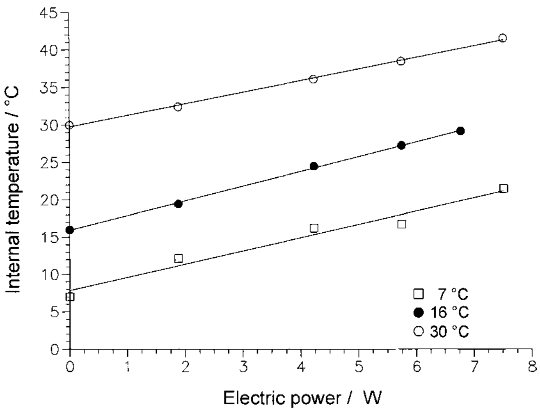

Fig. 2. Linear relationship between the electric power of the heater and the steady-state internal temperature of a *V. crabro* nest at three ambient temperatures.

internal temperature of a medium sized hornet nest. The slopes of the straight lines are identical in a first approximation and show the expected result that the temperature difference is directly proportional to the heating rate without any influence of the ambient temperatures.

From the known heat production rate P, the temperature gradient ΔT across the envelope as well as the surface A and the thickness Δx of the envelope, the thermal conductivity λ can be calculated from Fourier's law

$$P = -\lambda A \frac{\Delta T}{\Delta x}$$

Hornet nests from different seasons render $\Delta T/P$ ratios of 1.1–2.2, dependent on their sizes and ways of construction. While it is not too difficult to determine a mean Δx for the envelope the active surface area A is hard too estimate. In a first approximation spheres or prolate spheroids with a minimum surface were assumed. As A is inversely proportional to λ, the heat conductivities are overestimated in this way and may be smaller in reality by a factor of 1/2 or 1/3. With these ratios and specific envelope data the thermal conductivity is calculated to values ranging between 0.08 and 0.20 W (°C m)$^{-1}$. They are, thus, near to other insulating materials and similar to those of bird nests [14] listed in Table 1. This is somehow astonishing as bird nests have more homogeneous walls with smaller pores and a reduced air convection than that in the larger pockets of wasp nests. Comparison with the data from literature indicates that paper envelopes of hornet nests are a compromise between low mass or light weight and still low, but increased thermal conductivity due to air convection in larger spaces.

3.3. Infrared photography (thermography)

An other way of determining heat conductivity flow through nest envelopes is given by thermography when the surface temperature is monitored by optical means and the internal temperature by conventional thermometry. Fig. 3 shows an infrared photography of an active hornet nest at 18°C ambient temperature. The scale with different degrees of brightness at the right side indicates a temperature distribution of 2.5°C from dark at the top (23.2°C) to light at the bottom (20.7°C). The site of the used combs is clearly indicated by the darker area in the middle of the comb (about 22.4°C) demonstrating that the (bright) top comb is no longer used. A few air pockets contrast with lighter surfaces against the darker main envelope. The black spots of highest temperature (>23.2°C) are hornets working on the surface of the nest. The graph

Table 1
Heat conductivity of hornet nests compared with that of different insulating material (taken from different literature; the value of eider downs corresponds to that of still air)

Material	Heat conductivity (W (°C m)$^{-1}$)	Material	Heat conductivity (W (°C m)$^{-1}$)
Dry air	0.025	Cotton	0.058
Cork log	0.036	Different wood	0.12–0.21
Styrofoam	0.036	Paper	0.140
Silk (wooly)	0.036	Eider downs	0.023
Wool	0.036	Bird nest (great tits)	0.075
Glass fibre	0.042	Hornet nests	0.08–0.20

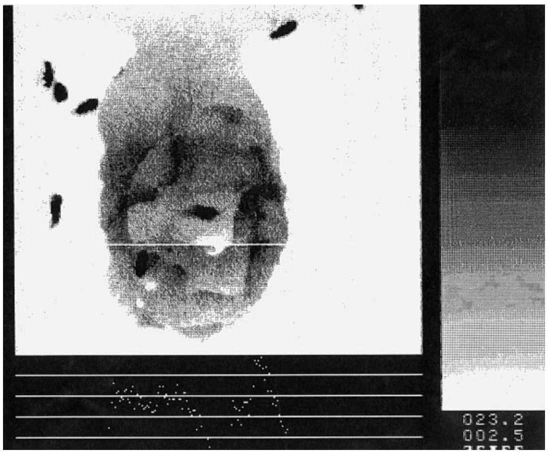

Fig. 3. Black-and-white thermographic picture of an active hornet nest at 18°C ambient temperature. For further information see text.

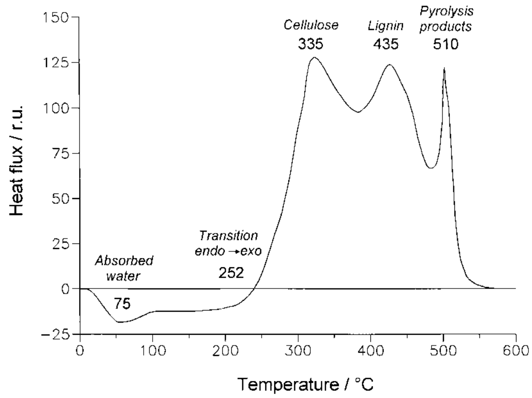

Fig. 4. DSC thermogram of a 2.2 mg sample from the nest envelope of a *V. vulgaris* nest. Scanning rate 20°C min^{-1}, normal atmosphere. The endothermic peak around 75°C corresponds to absorbed water, that at 335°C to pyrolysis of cellulose, at 435°C to that of lignin and at 510°C to the destruction of earlier pyrolysis products.

below the picture presents the temperature distribution along the white line in the photo with 0.5°C between two horizontal lines. The lowest temperature of the nest surface is still about 3°C above the ambient temperature pointing to the intensive heat production rate in the hornet nest.

Thermography is an interesting tool especially for the investigation of questions of energy metabolism and thermoregulation of social insects or insects in general but until now it is scarcely used [15,16]. This may be due to the fact that the spatial resolution of most cameras is not high enough for a good discrimination of the insects themselves. Of course, it would be without influence when only whole colonies or nests are investigated, e.g. at different times during the season and under varying ambient conditions.

3.4. Differential scanning calorimetry

DSC experiments were performed on hornet and wasp nests in the range of 30–600°C. Samples were taken from the different nest parts (pedicel, combs, envelope, silk, meconium) and from various points within them. It was never tried to make a homogeneous powder from larger sample masses and to use it as a *mean* specimen. Moreover, our DSC determinations did not allow for an appropriate ash determination after burning. Fig. 4 shows a representative DSC thermogram under air of a nest envelope of the wasp *Vespula vulgaris*. An endothermic peak due to the loss of absorbed water is observed at about 75°C, a transition from endothermic to exothermic effects around 252°C and three exothermic peaks around 335°C (cellulose), 435°C (lignin) and 510°C (supposedly components, e.g. char, formed during pyrolysis). It is known that combustion of cellulose proceeds in two steps: a gaseous combustion when the volatile degradation products of the low temperature part of pyrolysis catch fire (around 250°C) and a glowing combustion with evolution of CO, CO_2 and water when the carbonaceous residues like char pyrolyze (above 500°C) [17]. Since the thermogram shown in Fig. 4 originates from a run under air and not under nitrogen as in the TG curve (see below) significant differences appear between Figs. 4 and 5. As wasp nests are constructed from thousands of small wood particles of different origin, they are highly heterogeneous. Thus, larger variations in the height, the shape and the temperature of peaks may occur. Moreover, specific peaks may be missing when their corresponding wood structure was destroyed by weathering or microbial decay. The endothermic water peak is seen in all samples. Three fairly well separated exothermic peaks appear during pyrolysis under air. While the cellulose peak around 335°C is seen in envelopes, combs and pedicels, the high temperature peaks at 465 and 523°C are absent in the pedicel where a fourth peak (of pyrolysis products)

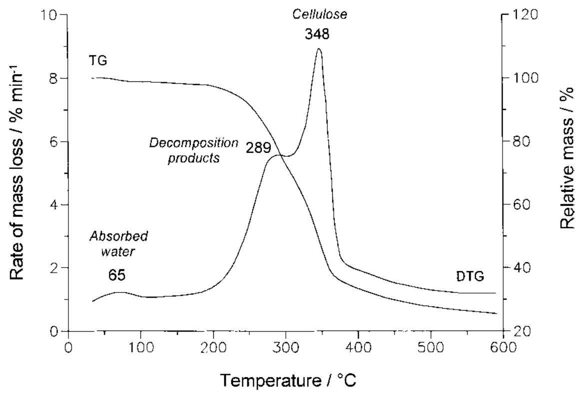

Fig. 5. Thermogravimetric curve (TG) and its first time derivative (DTG, i.e. the rate of mass loss) of a 3.57 mg sample from the envelope of a *V. crabro* nest, heating rate $10°C\ min^{-1}$ and gas flow rate $200\ ml\ min^{-1}$ nitrogen. The mass loss at 65°C corresponds to the release of absorbed water, that at 290°C to decomposition of hemicellulose and to that of cellulose at 348°C.

appears at 561°C. Meconium thermograms are significantly different from those of the other specimens. They offer a further endothermic peak at 222°C, a pronounced exothermic peak at 362°C and the main peak at 564°C. All three are not detectable in the carbohydrate determined curves of the nest. Charcoal thermograms under air have exothermic peaks at 480 and 533°C (as shoulder) well-known from the investigations of nest material. Under protecting gas flow these high exothermic peaks are missing and only a few weak endothermic peaks shine up (mainly at 130, 230 and 280°C). All three peaks are missing under air.

3.5. Thermogravimetry

Fig. 5 shows the curve of thermal decomposition of a nest envelope given as mass change together with the first time derivative, the rate of mass loss. The experiment was run in a combination of TG with mass spectrometry (MS) under nitrogen with a sample of 3.57 mg from the envelope of a *V. crabro* nest. Three distinct peaks of mass loss are decernible. Loss of absorbed, not chemically bound water appears between 60 and 110°C and amounts to 1.8% of the total mass, indicating the extremely low water content of the nest material (see Section 3.6). The corresponding values for the other components are 2.9% for the pedicel, 4.3% for the combs and 1.0% for chitin, all determined by TG.

The second peak around 290°C may be due to a decomposition of hemicellulose and a formation of volatile products and char [18], while the third one at 348°C is connected with the thermal degradation of cellulose, as often reported in the literature (for a review see [7]). This peak shifts to higher temperatures from combs and pedicels to envelopes and most distinctly to chitin. It shows that the thermal stability of the envelope is higher than those of the other components and more similar to that of chitin which decomposes around 375°C. It is astonishing that one further peak around 435°C connected with the pyrolysis of lignin is not observed in the TG/DTG curve.

The cellulose peak appears most pronounced and with the largest difference to the preceding one in envelope samples and least pronounced in pedicels (Fig. 6). Mass spectrometry shows that the most prominent fragments in this peak are *m/e*=18 (H_2O), 44 (CO_2) and 17 (OH, NH_3). The ratio H_2O/CO_2 is smallest for the envelope and largest for the combs in agreement with the determined water content. The essential fragment connected with nitrogen in the samples is *m/e*=27 (HCN); it appears most characteristically in chitin, followed by the pedicel and is significantly smaller in the envelopes and combs as already observed with solid-state [^{13}C] NMR by Espelie and Himmelsbach for *Polistes* nests [19]. They found a nitrogen concentration of 11% in the pedicel constructed from a mixture of carbohydrates and proteins. One of the main amino acids here is proline, well known as dominant component in many struc-

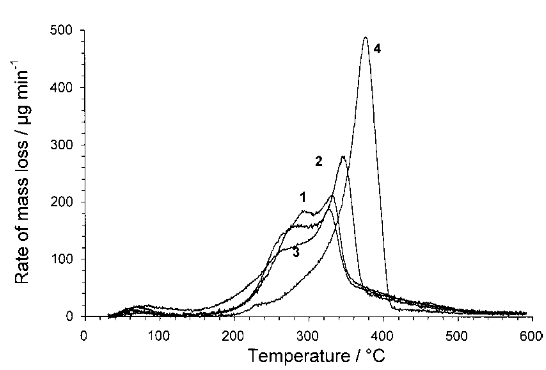

Fig. 6. Comparison of the rate of mass loss (DTG) curves of 1: the pedicel, 2: the envelope, 3: the comb and 4: chitin under nitrogen, heating rate $10°C\ min^{-1}$. The maximum mass loss of $490\ mg\ min^{-1}$ corresponds to a relative mass loss of $14\%\ min^{-1}$.

tural proteins. This confirms the entomological observation that most saliva cement is used in the construction of the nest support.

McGovern et al. found an inverse distribution of nitrogen in *Vespula* nests [3]. Following their chemical investigations the main organic compound in the envelope is cellulose (therefore the low nitrogen content of 1.36%). Cellulose fibers posses a high tensile strength against mechanical burden and a low specific weight. They are therefore very well suited for light nests and easy collecting activities. In contrast to the low value in the envelope the authors determined a high protein concentration in the combs (7.6% nitrogen). In general, nitrogen in the nest material not only originates from the proteinaceous glandular material of the adhesive but also from remainders of moulds responsible for the decay of wood which may be also seen between the fibers in electron microscopic pictures [3].

3.6. Ash, water and energy content of the envelope

The ash content of most nests is small (about 3%) comparable to or slightly higher than that of wood with the exception of nests of the wasp *Dolichovespula* (7.4%). Weathering wood increases its amount of ash considerably due to adsorption of dust from the air [3]. Thus, hornet nests may show the same increase in dependence of the source of wood fibres.

The water content of wasp nests is extremely low with only 3.6% in contrast to wood with more than 50% (fresh) and about 20% (dry), while the wood particles transported to the nest are really wet with humidities up to 80% [3]. This high water content presumably originates from the wasps' activity to separate small samples from a wood source. The later low amount of water in the nest material is of special importance for the insulating properties of the envelope. It was shown for bird nests that the water content of the wall material plays an essential role for heat conduction since it determines the relative humidity in the dead air spaces of the wall and since humid air has a significantly higher heat conduction as dry air. In the present experiments, the humidity in the wasp nests was not determined due to technical difficulties. But as the dead air spaces are completely surrounded by the dry wall material the obtained contribution to heat transfer should be small or even negligible. Moreover, the wasp spittel as adhesive mixed with the rotten wood during papermaking strengthens the waterproof quality of the material. Tests (own and from literature) showed that wasp paper may lie in water for a long time without taking up water or being decomposed in its individual wood particles [4].

The energy contents of the different nest components were determined by usual combustion calorimetry under high oxygen pressure. The obtained values for the envelope (-16.3 kJ g^{-1} DW), the combs (-17.3 kJ g^{-1}) and the pedicel (-18.2 kJ g^{-1}) are similar within the biological scatter and correspond to those for different kinds of wood [7,11]. As the ash content of nest material is very low (see above), the values presented above can be also taken as 'g^{-1} ash free DW'.

Only the combustion heat of meconium is significantly higher with a mean of -21.3 kJ g^{-1}. This value is astonishing high without any explanation for the reason. To our knowledge, the composition of meconium was never published, but it should mainly contain uric acid of low energy content (11.5 kJ g^{-1} [20]) together with chitineous remains of prey insects. Its DSC thermograms are completely different from those of the other nest parts with a lack of the typical peaks of carbohydrates and their pyrolysis products (see Section 3.4). Thus, it may be speculated that also some traces of fat are excreted by the hornets [21]. Nevertheless, meconium is a by-product of larval metabolism and development which reduces the fragility of the combs considerably without any further energetical costs for the hornets.

4. Conclusion

Construction of nests for sleeping, rearing the brood, forming the site of social life or establishing a special microclimate are widespread abilities in the animal kingdom. Thermal insulation — not only against cold, but also against overheating of the clutch of some tropical birds — is just one aspect of nest advantages besides protection against rain, ultraviolet light, strong irradiation or against predators.

Insect nests are formed from chewed wood as by the paper wasps investigated here, but also from clay or other mineral components or in a cocoon like form from silk. Some insects establish horizontal combs with cells opened downwards without any protecting envelope, other use holes in trees or the ground where the walls are lined in a similar way as with an envelope. It would be interesting to compare all these different nest forms, materials, chemical compositions and structures in their thermal properties by means of thermal analysis and to find common principles among or geographical differences between them. Further investigations in this direction — broadened by analysis of bird nests — are on their way.

Acknowledgements

We acknowledge with pleasure the support of our investigations by Dr. R. Kunze, D. Neubert and K. Brademann-Jock (Federal Institute for Materials Research and Testing, BAM, Lab. VI.11, Berlin, Germany) in performing the experiments with the coupled thermobalance/mass spectrometry system and the permission of Prof. Flesch and Mrs. Engel (University Clinicum Rudolf Virchow, Free University, Berlin, Germany) to take infrared pictures of hornet nests in their department.

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