The parietal association of Diptera in two man-made subterranean shelters: a limestone mine and a bomb-shelter

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The dipteran fauna of a limestone mine and a bomb-shelter in Denmark was dominated by hibernating *Culex*-mosquitoes (primarily *Cx. pipiens* Linnaeus) and *Culiseta annulata* Schrank (Culicidae), *Heleomyza serrata* (Linnaeus) (Heleomyzidae), and fungus-gnats (Mycetophilidae). In the mine the number of *Culex*-mosquitoes was negatively correlated with the distance from the entrance. Heleomyzids mainly occurred 15-50 metres from the entrance. In the innermost galleries practically no dipterans were observed. In the bomb-shelter *Culex*-mosquitoes and *Cs. annulata* were primarily recorded from the exterior section. The two shelters were occupied by a parietal association of habitual trogloxenes. A strong resemblance between the dipteran fauna of the two sites and the parietal association observed in caves and mines throughout Europe was found.

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Introduction

The insect fauna of European caves and mines has been extensively studied and the species categorized according to habitat relationship. In caves a number of habitats and corresponding species associations are distinguished, among these the cave threshold and the insect species occurring on walls and roof near the entrance – the so-called parietal association (Jeannel, 1926). This fauna is dominated by dipterans (Jefferson, 1983). Only a few species of Diptera recorded from caves in northern Europe are considered obligate cave-dwellers (troglobites) or seem capable of building up permanent, reproducing populations in subterranean as well as above ground habitats (troglophiles). However, the majority of the species utilizes the caves as a temporary shelter only (habitual trogloxenes), e.g. for hibernation or aestivation or they occur accidentally (accidental trogloxenes).

In Denmark caves are rare and confined to a few man-made limestone mines in Jutland. Though limestone mining in some cases dates at least as far back as the early Middle Ages, the resulting caves are very young on a geological time scale. No information on the dipteran fauna of Danish limestone mines are available. However, it is expected that these cave systems are mainly utilized by a parietal association of habitual trogloxenes, above all hibernating species, i.e. a dipteran fauna comparable to that of cellars, bomb-shelters, etc. This paper reports on Diptera observed in a limestone mine and an abandoned bomb-shelter and on the temporal and spatial distribution of predominant species.

Materials and methods

Field sites

Smidie: An abandoned limestone mine situ-

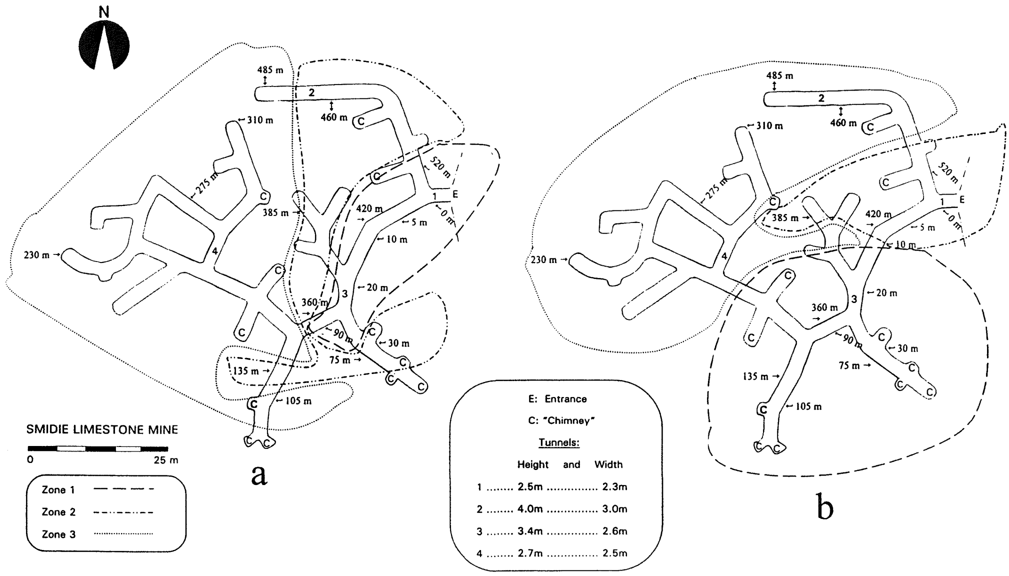

Fig. 1. Smidie limestone mine. Distribution of Culex-mosquitoes (a) and *Heleomyza serrata* (Heleomyzidae) (b), 1985-1990. Zone 1 and 3 highest and lowest prevalence respectively. "Chimneys" are sinks, where the miners unintentionally broke through the limestone and into the top soil, constituting an obstacle to further mining. Sketch redrawn after Sloth and Christensen 1974.

ated 1 km NE of the village of Smidie, northeastern Jutland (UTM: 32VNJ705033). The mining started in 1857 (Heilskov, 1930-32), came gradually to an end in this century and in 1978 the site was designated as a preserved locality. The main section of the horizontal galleries (total length: 265 m, Fig. 1) originates from a single entrance dug into the face of a hillside, facing the East. In this direction extensive pastures traversed by ditches are found, 2 km further east adjoining the moorland Lille Vildmose. The galleries of the mine, which contain very little dead organic matter, generally run only a few metres below the surface of the ground. Along the two walls of the galleries, markers are placed at intervals of 5 m (consecutive numbering); at 15 m, 230 m, and 485 m max.-min. thermometres are permanently installed. At each visit air temperature and humidity (RH) were measured at a number of additional positions in the mine as well as outside the entrance. The temperature and RH of the mine (15-485 m) are very stable, i.e. 6.0-8.5°C and >97% all the year round. The limestone may absorb great amounts of water, thus the walls are moist and during periods of heigh precipitation large drops of percolated water are formed on the walls and ceiling. In the main gallery (0-15 m, Fig. 1) easterly winds may create a just perceptible drought, not penetrating into the inner tortuous galleries. Daylight is only noticeable in the extreme 0-10 m of the main gallery.

Gl. Rye: A ferro-concrete bomb-shelter (height: 3 m, width: ca 14 m, length: ca 26 m, raising 0.75 m above ground level, Fig. 2) constructed during World War 2. The site is situated in a woodland edge 6.5 km SW of the village of Gl. Rye, Central Jutland (UTM: 32UNH422122). Towards the North and the West the bomb-shelter faces agricultural land, towards the South and the East it is surrounded by coniferous forest. A northern and a southern way of access lead to the interior of the bomb-shelter and still one to a separate exterior room (no.1). Eleven air

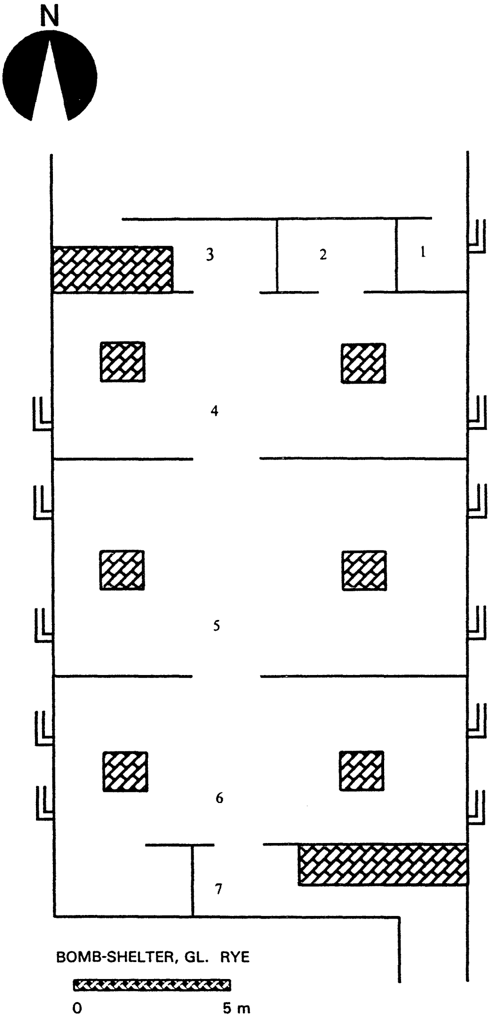

Fig. 2. Floor plan of the bomb-shelter at Gl. Rye. In the text rooms 4, 5 and 6 are referred to as "inner bomb-shelter"; the eleven air shafts are shown. Redrawn after plan by Birger Jensen.

shafts once leading to the open are now overgrown or filled with rubble. However, throughout the year there is free access for fresh air through the two main entrances. At each visit, air temperature and RH were measured outside the northern entrance, in room no. 1, and in the interior of the bomb-shelter. Data on macroclimatic factors were obtained from The Danish Meteorological Institute (station: Himmelbjerget). The air temperature of the bomb-shelter varies according to the ambient temperature, fluctuations, however, being damped and delayed (Andreasen, 1991). In autumn-spring the floor of the bomb-shelter is nearly permanently covered by 20-25 cm of water and mud and the lower parts of the walls are constantly damp. During October 1987-May 1988 RH < 95% was never observed. Depending on wind force and direction, draught is induced in the interior of the bomb-shelter. The darkest and most sheltered section is room no. 2, the most illuminated one room no. 1.

Field observations and sampling

The limestone mine (21 visits, 1983-1990) and the bomb-shelter (27 visits, 1985-1991) were inspected by torch light between August-September and early May. Further, an annual visit was paid in June-July. The main studies were done in 1987-1988 (mine: 2 visits in autumn, 2 in winter, 3 in spring; bomb-shelter: 2 in autumn, 2 in winter, 7 in spring). In the mine the predominant dipterans, i.e. mosquitoes and heleomyzid flies (Heleomyzidae) were counted in 27 plots (area: 2 m^2) evenly distributed on the whole mine-system and insects were collected in 6 additional plots (area: 2 m^2). In the bomb-shelter mosquitoes were counted in 16 plots on walls and ceiling of the rooms and the numbers expressed per m^2. Dipterans were sampled in 2 plots (area: 6 m^2) in room no. 2 and 6. All dipterans were collected by means of a battery-powered aspirator.

Laboratory work

Female *Culex*-mosquitoes were examined for the presence of *Culex pipiens* Linnaeus and *Culex torrentium* Martini, dissected, and gonotrophic stage and development of fat body recorded (Andreasen, 1991; Andreasen & Nielsen, in prep.). The two species were tentatively separated according to Onyeka (1982) and Jaenson (1987), i.e. females without pre-alar scales (or scale insertions) on either side were denoted as *Cx. pipiens*, specimens with >4 scales (or insertions) on one

Table 1. Dipterans collected in a limestone mine (Smidie) and a bomb-shelter (Gl. Rye), Denmark, August-May 1983-1991.

Taxon	Limestone mine		Bomb-shelter	
	♂	♀	♂	♀
Culicidae				
Culex spp.	0	1515	0	1064
Culiseta annulata Schr	0	7	0	206
Anopheles maculipennis s.l.	0	0	0	12
Mycetophilidae				
Exechiopsis subulata (Winn.)	5	1	9	6
E. intersecta (Mg.)	1	2	0	1
E. indecisa (Walk.)	9	6	6	2
Rymosia fasciata (Mg.)	1	2	66	40
Pseudexechia trivittata (Stæg.)	0	0	1	2
Tarnania fenestralis (Mg.)	0	0	10	20
Mycetophila signatoides Dzied.	1	0	6	3
Chaoboridae				
Mochlonyx martini Edw.	0	0	6	6
Dixidae				
Dixella aestivalis Mg.	0	0	0	1
Scatopsidae				
Scatopse notata (L.)	0	1	0	0
Psychodidae				
Psychoda phalaenoides (L.)	0	0	0	1
Limoniidae				
Limonia nubeculosa (Mg.)	3	0	5	2
Phoridae				
Megaselia sp.	0	0	0	2
Heleomyzidae				
Heleomyza serrata (L.)	242	205	0	5
Scoliocentra villosa Mg.	6	3	2	0
Drosophilidae				
Drosophila busckii Coquill.	0	0	0	1
Sphaeroceridae				
Crumomyia fimetaria (Mg.)	0	0	1	0
Total	2010		1486	

side as *Cx. torrentium*, and those with 1-4 scales (or insertions) on one side and 0-4 on the other as *Cx. pipiens/Cx. torrentium.*

Results

Species composition

In the limestone mine and the bomb-shelter, female *Culex*-mosquitoes were the predominant dipterans collected, contributing 72-75% (Table 1). In both sites mosquitoes denoted as *Cx. pipiens* were predominant, a considerable proportion was *Cx. pipiens/Cx. torrentium*, and only a small number might represent *Cx. torrentium* (Table 2).

In the bomb-shelter overwintering female *Culiseta annulata* were second (13.9%), in the mine, however, they were few in number, while male and female *Heleomyza serrata* were the second most abundant dipteran (22.2%). In the bomb-shelter male and female Mycetophilidae (7 species) were rather abundant (11.6%), in the mine, however, only a few fungus-gnats (5 species) were collected. All remaining dipteran taxa recorded in the two sites were infrequent.

Table 2. Taxonomic composition (% ranges) of hibernating *Culex* mosquitoes collected in a limestone mine (Smidie) and a bomb-shelter (Gl. Rye), 1985-1989.

Site	Nos of samples	n	*Cx.pipiens*	*Cx.pipiens/ torrentium*	*Cx.torrentium*
Mine	8	415	61.4-70.5	29.5-38.6	0.0-4.0
Bomb-shelter	16	587	56.5-81.8	18.2-40.0	0.0-5.7

Spatial distribution and seasonal abundance

In the mine and the bomb-shelter a total of 7.397 (1983-1990) and 16.185 (1985-1991) *Culex*-mosquitoes were counted, respectively. The numbers of *Culex* counted in the mine 1987-1988 were first tested for normality using the Shapiro-Wilk and the Kolmogorov-Smirnov tests. Then parametric or non-parametric tests were employed as appropriate. All tests were carried out at significance level $p = 0.05$. A Friedman two-way Anova and subsequently a multiple range test (Student-Newman-Keuls test) was performed on the ranked data. A significant difference between the numbers counted at different locations in the mine ($\chi^2 = 287.67$, df = 26, $p<0.001$) and in the seasonal variation of mosquitoes recorded at the different locations was found (Kendall coefficient of concordance (W), W = 0.71, df = 26, $p<0.001$). According to the multiple comparison analysis of the numbers counted in 1987-1988, the locations could be subdivided into three homogeneous zones (Fig. 1a) with descending mosquito counts. A similar distribution pattern was observed in 1985-86 and 1989-90. In 1987-88 there was a significant negative correlation between the numbers of mosquitoes counted and the distance from the entrance (Spearman rank-correlation coefficient (r_s), $r_s = -0.64$, n = 519, $p<0.001$) and between the zones (1-3) and the numbers of mosquitoes counted ($r_s = -0.65$, n = 593, $p<0.001$). The mosquitoes mainly occurred in the exterior part of the main gallery, whereas very few specimens were observed in the inner galleries. Within the zones the negative correlation was significant within zone 1 ($r_s = -0.20$, n = 219, $p<0.01$) and zone 3 ($r_s = -0.35$, n = 150, $p<0.001$), but not within zone 2 ($r_s = -0.12$, n = 150, $p>0.05$).

In autumn, winter, and early spring, the density of mosquitoes in the bomb-shelter (1987-1988) was distinctly higher in room 2 (12.3-29.7 m^{-2}) than in room 3 (0.1-5.6 m^{-2}) and the inner bomb-shelter (room 4-6, 0.6-3.0 m^{-2}). In room 1 and 3 maximum densities of mosquitoes, i.e. 11.8-14.3 m^{-2} and 5.6 m^{-2} respectively, were observed in autumn and early winter, however, the abundance fluctuated according to wind direction and minimum temperature. In room 7 the number of mosquitoes counted was very low, thus the densities were not estimated.

In *Culex*, the times of immigration to and emigration from the hibernation sites did not vary between years, as judged by increasing and decreasing numbers. The immigration commenced in mid August-early September and maximum numbers were reached in November. During the winter the number of *Culex* hibernating in the mine was reduced drastically due to fungal infection by *Entomophthora destruens* Weiser & Batko (Andreasen, 1991; Andreasen & Nielsen, in prep.). From November to February-March 1985-86, 1987-88, and 1989-90, the densities of *Culex* mosquitoes in all zones declined from 34.8, 11.2, and 20.5 m^{-2}, respectively, to 2.2, 2.3, and 2.9 m^{-2}, respectively. In spring 1988, all mosquitoes surviving hibernation in the mine emerged over a period of no more than 5 days during late April-early May, from the bomb-shelter, however, they emigrated steadily throughout May. In the two sites, no *Culex* were observed in June-July.

In the two shelters, overwintering *Cs. an-*

nulata were recorded from early September to early May, the main immigration occurring in November. Within the same period a few *Anopheles maculipennis* s.l. occurred in the bomb-shelter. Even in mid-winter *Cs. annulata* mainly occupied room no. 1 of the bomb-shelter, e.g. in late January 1988 >52% of all mosquitoes were counted in this room and only ca 13% in the inner bomb-shelter (n = 367). No *Cs. annulata* were observed in June-August.

In the mine a significant difference in the number of heleomyzids (1983-1990; n = 2.433) counted at different locations (n = 27) in the galleries 1987-1988 was found (Friedman two-way Anova, $\chi^2 = 176.67$, df = 26, p<0.001). Further, the seasonal variation of flies recorded at the plots differed significantly (W = 0.52, df = 26, p<0.001). According to the multiple comparison analysis of the ranked data from 1987-1988 the locations could be divided into three homogeneous zones with descending fly counts (Fig.1b). Heleomyzids mainly occurred in the interior section of the main gallery and the outer parts of the central galleries (15-50 metres from the entrance). In the innermost galleries, however, they were only sporadically observed. A similar distribution pattern was recorded in 1985-86 and 1989-90. There was a significant negative correlation between the number of flies counted in 1987-88 and the distance from the entrance ($r_s = -0.16$, n = 519, p<0.001). Within the zones the negative correlation was significant within zones 2 and 3 (2: $r_s = -0.144$, n = 214, p<0.05; 3: $r_s = -0.28$, n = 112, p<0.01), but not within zone 1 ($r_s = -0.08$, n = 193, p>0.05). Heleomyzid flies were observed from August-September to April, the numbers declining throughout the winter mainly due to fungal infection. In May-July no living flies were found in the galleries.

In the bomb-shelter, the predominant fungus-gnat *Rymosia fasciata* (n = 106, ca 62% of all mycetophilids) was collected every month from September to May, the majority (ca 63%) being recorded in December-January. In the two sites *Limonia nubeculosa* was observed and collected from mid August to early September. In the bomb-shelter the chaoborid *Mochlonyx martini* was recorded in September-October (9 individuals) and February (3 individuals).

Discussion

The insect fauna of the limestone mine is dominated by culicids, heleomyzids, and fungus-gnats, which coincides with observations from the thresholds of most caves and mine-systems studied throughout Europe (e.g. Tollet, 1959; Matile, 1970; Jefferson, 1983; Kjærandsen, 1993). A similar dipteran association is observed in the bomb-shelter. No doubt, the use of traps would increase the list of species recorded (cf. Kjærandsen, 1993), however, no abundant species are expected. Evidently, female *Cx. pipiens*, *Cs. annulata*, and *An. maculipennis* are habitual trogloxenes using the shelters for hibernation. In temperate regions diapausing, inseminated *Cx. pipiens* often hibernate in high densities in natural or man-made shelters like caves, mines, cellars, and outbuildings (Wesenberg-Lund, 1920-21; Kryger, 1930; Lerouth, 1939; Mohrig, 1969; Kühlhorn, 1983a, 1983b; Sulaiman & Service, 1983; Jaenson, 1987; Cranston et al., 1987). *Cx. pipiens* mainly occurs near the entrance of the limestone mine, where daylight is still perceptible. Apparently, photoperiod is an important external factor regulating ovarian development and hibernation (Clements, 1992). In the bomb-shelter, the highest densities of mosquitoes were recorded in the darkest but most sheltered room. According to Cranston et al. (1987) fluctuating winter conditions in the shelters may cause movements of *Cx. pipiens*. In the bomb-shelter hibernating *Cx. pipiens* moved between the walls of room no. 1 and an air shaft, concurrently with temperature fluctuations (Andreasen, 1991).

Females of the two sibling species *Cx. pipiens* and *Cx. torrentium* are not easily separated. A number of diagnostic characters have been described to separate the two species: wing venation (e.g. Natvig, 1948) and the number of pre-alar scales (Mattingly, 1951).

However, none of these characters provide an unambiguous identification of *Cx. pipiens* and *Cx. torrentium* (Service, 1968; Onyeka, 1982; Sulaiman & Service, 1983). Nevertheless, pre-alar scales (often 4 or more) are normally present in *Cx. torrentium* and usually absent (not more than 2, if present) in *Cx. pipiens* (Sulaiman & Service, 1983; Cranston et al., 1987). However, females of the two species can only be unambiguously identified by allozyme patterns (Urbanelli et al., 1981) or by identifying F_1-males (Sulaiman & Service, 1983). Probably, a few *Cx. torrentium* were present in the two shelters. According to Sulaiman & Service (1983) the principal winter quarter of this species remains unknown, however, Jaenson (1987) records hibernating specimens from a cellar.

Cs. annulata hibernates in cellars, cool buildings, hollow trees, etc., often together with *Cx. pipiens*, though less numerous than the latter species (Wesenberg-Lund, 1920-1921; Kryger, 1930; Mohrig, 1969; Kühlhorn, 1974, 1987). In 1987-1988 maximum number of the species did not occur until the winter period. Apparently, *Cs. annulata* is active later in the year than is *Cx. pipiens* (Wesenberg-Lund, 1920-1921; Kühlhorn, 1987).

The heleomyzid *H. serrata* has been recorded from caves throughout Europe (e.g. Wolf, 1934-38; Lerouth, 1939; Dixon, 1974; Hazelton, 1975; Østbye et al., 1987; Kjærandsen, 1993). In the limestone mine at Smidie the species is abundant in late summer and autumn, however, during the winter a very high mortality due to fungal infection is observed. High mortality in *H. serrata* in caves and mines is also recorded by Tollet (1959), Jefferson (1983), and Kjærandsen (1993) and the incidence of fungal infections by Teernstra-Eeken & Engel (1967). Though overwintering male and female *H. serrata* are abundant in the limestone mine, no larvae are observed. *H. serrata* breeds in dung, e.g. bat dung. Though many bats hibernate in the mine, conspicuous deposits of bat dung are not accumulated during the winter period, excrements occurring scattered on the wall and floor. Thus the fly population observed in the mine is seemingly build up annually, resulting from above-ground reproduction. In most European cave systems, including the Danish limestone mine, *H. serrata* is a habitual trogloxene (e.g. Tollet, 1959; Østbye et al., 1987; Kjærandsen, 1993). In a cave in North-West England *H. serrata* mainly occurred at a distance of 30-75 m from the entrance (Dixon, 1974). A similar pattern was observed in this study, the species mainly being abundant in the outer section of the dark zone of the mine.

In European caves Mycetophilidae is a predominant taxon (e.g. Tollet, 1959; Kjærandsen, 1993). All species recorded from the limestone mine and the bomb-shelter are previously known from European cave systems (e.g. Wolf, 1934-38; Lerouth, 1939; Kjærandsen, 1993). The predominant species *R. fasciata* is abundant in European caves (Matile, 1970). Several species of Mycetophilidae overwinter in e.g. cellars, outbuildings, and caves (Hutson et al., 1980). The species from cave thresholds are considered habitual trogloxenes (Kjærandsen, 1993).

The crane-fly, *L. nubeculosa*, which is recorded from both shelters in mid August-early September, is associated with cave thresholds in Britain, continental Europe, and USA (Tollet, 1959; Kjærandsen, 1993). *L. nubeculosa* is considered a habitual trogloxene, in the Palaearctic region aestivating in subterranean shelters (Matile, 1970; Jefferson, 1983; Kjærandsen, 1993). The remaining dipteran taxa (Table 1) are probably accidental trogloxenes or opportunistic species.

The investigation demonstrates that the dipteran fauna of the limestone mine at Smidie constitutes a parietal association dominated by habitual trogloxenes. No troglobites or troglophiles are found. The species mainly occur near the entrance, in the innermost galleries practically no insects are observed. Excepting *L. nubeculosa*, the association recorded is composed of hibernators. With a few exceptions, the insect species observed in the limestone mine are previously recorded from several other European cave systems, again illustrating the strong resemblance between the parietal association observed in caves and mines throughout Europe.

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Dansk sammendrag

Insektfaunaen i europæiske huler og minesystemer er flittigt udforsket. På hulernes vægge og loft nær indgangen findes en særlig fauna domineret af dipterer. Disse arter udnytter blot hulerne midlertidigt til overvintring eller oversomring, mens nogle kun er tilfældige gæster. I Danmark er hulesystemer repræsenteret ved de jyske kalkminer. Insektfaunaen her er ikke tidligere studeret, men ud fra erfaringer fra huleforskning i udlandet og de danske miners beskedne alder måtte det forventes, at de primært husede overvintrende dipterer. Nogle af disse arter udnytter også andre kunstige underjordiske gemmesteder, f.eks. kældre. I en kalkgrube ved Smidie, Østhimmerland og i en stor, tysk kommandobunker (fra 2. verdenskrig) ved Gammel Rye, Midtjylland udgjorde stikmyg (♀♀) af slægten *Culex* 72-75% af insektfaunaen. Den lille husmyg (*Culex pipiens*) dominerede, men antagelig var *Cx. torrentium* repræsenteret ved nogle få individer; morfologisk artsbestemmelse af *Culex*-hunner er dog usikker. I minen og bunkeren var henholdsvis sumpfluer (*Heleomyza serrata*, Heleomyzidae, ♂♂,♀♀) og den store husmyg (*Culiseta annulata*, ♀♀) næsthyppigst. I bunkeren var hanner og hunner af svampemyg (Mycetophilidae, 7 arter) også talrige. I kalkminen sad *Culex*-myggene især i hovedgangen; antallet faldt signifikant fra indgangen ind gennem gangsystemet. Yderst få observeredes i de indre gange. Indvandring af *Culex*-hunner startede midt i August-begyndelsen af September og antallet af overvintrende myg toppede i november. I Smidie kalkmine faldt antallet i vinterens løb p.g.a. svampeinfektion (*Entomophthora destruens*). De overlevende myg udvandrede i april-maj. *Culiseta annulata* observeredes fra september til maj; hovedinvasionen fandt først sted i november. I bunkeren var arten især knyttet til de ydre rum. I minen observeredes sumpfluer (Heleomyzidae) fra august-september til april; svampeinfektion reducerede antallet drastisk i vinterens løb. Sumpfluerne sad især i 15-50 meters afstand fra indgangen, hvor der var helt mørkt. I årets løb udnyttes de to menneskeskabte, underjordiske lokaliteter øjensynligt kun midlertidigt af fluer og myg – først og fremmest af overvintrende arter. Muligvis oversomrer stankelbenet *Limonia nubeculosa* her, mens enkelte dipterarter sikkert er tilfældige gæster eller opportunister. På begge lokaliteter svarede dipterfaunaens artssammensætning godt til den vægfauna, der er observeret nær indgangen i huler og minesystemer mange steder i Europa.

taxonomer sandsynligvis vil blive billedanalyse-specialister og computerprogrammører, der kan scanne måske hundreder af arter om dagen. Teknologien vil udover at sortere og beskrive arterne skabe fylogenetiske træer baseret på den scannede morfologi. Suppleret med genetisk kortlægning ville der være en kraftfuld teknologi til at identificere geografiske områder for naturlighed, som artsdynamoer og som endemisk særlige områder." I løbet af nogle årtier vil der endog være mulighed for at genskabe naturlige kredsløb og udsætte arter efter en global klimaforandring, hævder Samways.

På alle niveauer af insektbevarelse – fra tilvejebringelse af grundviden til den praktiske udførelse af projekter – står og falder alt imidlertid med den offentlige og politiske erkendelse af biodiversitetens betydning. Insekternes talsmænd behøver da en solid og bred videnskabelig referenceramme i ryggen, og her har Samways leveret en lødig og velafbalanceret grundbog.

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