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Increased cave use by butterflies and moths: a response to climate warming?

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Abstract: Between 2015 and 2019, the list of Lepidoptera from "cave" habitats (i.e., proper caves, rock shelters and artificial subterranean structures) in Austria grew from 17 to 62 species, although the effort of data collection remained nearly constant from the late 1970s onwards. The newly recorded moths and butterflies were resting in caves during daytime in the the warm season, three species were also overwintering there. We observed *Catocala elocata* at 28 cave inspections, followed by *Mormo maura* (18), *Catocala nupta* (7), *Peribatodes rhomboidaria*, and *Euplagia quadripunctaria* (6). More than half of the species have been repeatedly observed in caves in Austria or abroad, so their relationship with such sites is apparently not completely random. Since the increase of records in Austria coincided with a considerable rise in the annual number of hot days (maximum temperatures ≥30°C) from 2015 onwards, we interpret the growing inclination of certain Lepidoptera towards daytime sheltering in caves as a behavioral reaction to climate warming.

Keywords: Lepidoptera, cave use, diurnal retreat, refuge-site preference, climate change

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INTRODUCTION

In most cave fauna surveys butterflies and moths are underrepresented except for a handful of common subtroglophile species such as *Scoliopteryx libatrix* and *Triphosa dubitata*. This shortcoming pertains particularly to species that sporadically use caves and cave-like spaces for sheltering during daytime. The reason is double: Cave mouths and rock shelters are not in permanent darkness, hence many biospeleologists do not understand them as subterranean habitats (Culver & Pipan 2009, Mammola et al. 2019). And, second, trogloxenes (*sensu* Sket 2008) have been largely neglected as irrelevant vagrants.

The list of Austrian "cave Lepidoptera" grew only slightly from 13 to 17 species in three deacades after the last compilation (Christian & Moog, 1982). During that period, vast numbers of zoological cave inspections by the present authors yielded no further lepidopteran species record from a cave: the inventory appeared fairly complete. Thus it was unexpected when we observed, in mid-summer of 2015, two specimens of the tiger moth *Euplagia quadripunctaria* in a cave south of Vienna (Christian et al., 2017). Daytime sheltering in caves of this species had been reported from warmer climate regions but not from Central Europe. Two weeks later we met four specimens of *Catocala elocata* resting in a shallow cave in Eisenstadt (Burgenland), also the first such observation in Austria. From 2015 to 2019 we eventually found 45 lepidopteran species for the first time in subterranean cavities. In the present paper we compile all butterfly and moth species from Austrian caves and present those recorded for the first time in more detail. We specify the respective type of cave use and suggest a possible driver behind the evidently increasing attractivity of caves for Lepidoptera, namely the annual number of hot days as a consequence of climate warming.

MATERIALS AND METHODS

Data come chiefly from protocols of long-term cave inspections by two of us (OM & EC) in eastern Austria (Burgenland, Lower Austria, Vienna) and occasional inspections in other provinces (Table 1). Inspections took place in daylight. A few records (verified by us) have been contributed by speleologists. Both local and temporal inspection density was highest along the eastern Alps boundary and in the hill ranges

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east of the Vienna Basin, at elevations from the planar to the submontane life zone. A round dozen of localities were inspected once or several times a year, the rest sporadically. Habitats included natural objects such as proper caves (Curl, 1964), shelter caves and spacious rock overhangs, as well as man-made structures such as air raid shelters, mines, tunnels and river underpasses. Natural and artificial underground spaces are collectively termed "caves" hereafter. According to Trimmel (1968) we let a cave begin at the eaves line, i.e., the horizontal projection of the edge of the rock that roofs the cave mouth. In artificial objects rock was sometimes replaced by a brick or concrete lining.

Lepidoptera were identified in place or determined on the basis of *in situ* photographs. Moths without distinct external features were taken to the laboratory for closer inspection. Specimens that required genital dissection were stored deep-frozen until examination by P. Buchner, who posted several photos and data on the Lepiforum web pages. Locations are detailed in Table 1.

Table 1. Locations of Lepidoptera reported for the first time from caves in Austria. Left column: Token with indication of the state (B: Burgenland, C: Carinthia, L: Lower Austria, S: Styria, T: Tyrol, U: Upper Austria, V: Vienna). Objects registered in the Austrian cave cadastre are designated by the full cadastral number (e.g., 1917/4); for any other object the appropriate cadastral area is stated (e.g., 1917/-).

	Location	**Type, Cadastral area or cad. #**	**Municipality**	**Geogr. coord. MGI [°N, °E]**	**Altitude [m asl]**
V1	Schreiberbach	Underpass, 1917/-	Vienna	48.2590, 16.3518	215
V2	Krapfenwaldbach	Underpass, 1917/-	Vienna	48.2669, 16.3319	330
V3	Nesselbach „B 1935"	Brook tunnel, 1917/-	Vienna	48.2688, 16.3197	375
V4	Nameless headwater	Brook culvert, 1917/-	Vienna	48.2747, 16.3217	425
V5	Gspöttgraben	Underpass, 1917/-	Vienna	48.2571, 16.3139	305
V6	Tunnel to artesian well	Brick vault, 1917/-	Vienna	48.2436, 16.3556	185
L1	Kaltenleutgebener Höhle	Cave, 1917/4	Kaltenleutgeben	48.1243, 16.2185	325
L2	Merkurhöhle	Cave, 1917/5	Kaltenleutgeben	48.1243, 16.2182	325
L3	Loess cellar Rehgraben	Cellar, 6848/-	Langenzersdorf	48.3910, 16.3643	205
L4	Piesting culvert under L 157	River culvert, 1921/-	Tattendorf	47.9318, 16.3322	225
L5	Marienbründl	Well house, 1921/-	Moosbrunn	48.0147, 16.4749	180
L6	Hochbergkeller	Cellar, cave, 1915/-	Perchtoldsdorf	48.1154, 16.2676	265
L7	Excentriqueshöhle	Cave, 1815/37	Kaltenleutgeben	48.1219, 16.2244	348
L8	Gaisberghöhle	Cave, 1815/6	Kaltenleutgeben	48.1118, 16.1992	476
L9	Östliche Mistelhöhle	Cave, 1915/13	Maria Enzersdorf	48.0877, 16.2764	305
L10	Westliche Mistelhöhle	Cave, 1915/14	Maria Enzersdorf	48.0877, 16.2763	305
L11	Einödhöhle	Cave, 1914/6	Pfaffstätten	48.0253, 16.2368	375
L12	Hinterbrühlerhöhle	Cave, 1914/13	Hinterbrühl	48.0823, 16.2424	305
L13	Hinterbrühler Felsentor	Cave, 1914/12	Hinterbrühl	48.0834, 16.2449	300
L14	Schüttkastenhöhle	Cave, 1913/14	Heiligenkreuz	48.0554, 16.1305	315
L15	Tunnel close to Lourdes grotto	Artificial tunnel, 1913/-	Heiligenkreuz	48.0553, 16.1308	310
L16	Wasserglurn	Adit and cave, 1913/12	Heiligenkreuz	48.0311, 16.1384	285
L17	Nameless small cave	Cave, 1912/-	Baden	48.0116, 16.2306	295
L18	Winschloch	Cave, 1912/35	Baden	48.0163, 16.2271	310
L19	Harzberg sand tunnel no. 1	Disused mine, 1911/-	Bad Vöslau	47.9683, 16.1943	390
L20	Harzberg sand tunnel no. 2	Disused mine, 1911/-	Bad Vöslau	47.9684, 16.1942	390
L21	Schelmenloch	Cave, shelter, 1911/41	Bad Vöslau	47.9819, 16.1985	330
L22	Schelmenloch cella	Rock tunnel, 1911/-	Bad Vöslau	47.9819, 16.1988	330
L23	Guglzipfhöhle	Cave, 1869/1	Berndorf	47.9427, 16.1120	350
L24	Höllturmhöhle	Cave, 1869/7	Wöllersdorf	47.8681, 16.1755	355
L25	Steinwand rock shelter	Deep overhang, 1818/-	Furth / Triesting	47.9309, 15.9439	660
L26	Steinwandklamm-Halbhöhle	Cave, 1868/47	Furth / Triesting	47.9319, 15.9485	570
L27	Wegkluft	Cave, 1868/49	Muggendorf	47.9316, 15.9444	665
L28	Türkenloch	Cave, 1868/4	Muggendorf	47.9306, 15.9452	695
L29	Pecherhöhle	Cave, 1868/3	Muggendorf	47.9305, 15.9451	695
L30	Hofmannshöhle	Cave, 1864/8	Wöllersdorf	47.8557, 16.1460	500
L31	Trockenes Loch	Cave, 1836/34	Schwarzenbach	47.9134, 15.3743	760
L32	Templerhöhle	Cave, 2872/20	Seebenstein	47.6966, 16.1492	415
L33	Karnerhöhle	Cave, 2872/5	Pitten	47.7171, 16.1899	380
L34	Tunnel below Hainburg Castle	Air raid shelter, 2921/-	Hainburg	48.1425, 16.9467	225

L35	Danube bank tunnel no. 1	Rock tunnel, 2921/-	Hainburg	48.1537, 16.9475	145
L36	Danube bank tunnel no. 2	Rock tunnel, 2921/-	Hainburg	48.1541, 16.9478	145
L37	Rötelsteinhöhle	Rock tunnel, 2921/6	Hainburg	48.1534, 16.9606	335
B1	Ludlloch	Cave, 2911/1	Winden am See	47.9707, 16.7558	190
B2	Hartllucke	Cave, 2911/38	Eisenstadt	47.8565, 16.5274	250
B3	Kleine Hartllucke	Cave, 2911/39	Eisenstadt	47.8569, 16.5275	250
B4	Flache Hartllucke	Cave, 2911/40	Eisenstadt	47.8571, 16.5275	250
B5	Johannesgrotte	Cave, 2911/25	Eisenstadt	47.8633, 16.5221	290
B6	Sulzbergschluf	Cave, 2911/43	Stotzing	47.8968, 16.5312	320
B7	Kirchenhalbhöhle	Cave, 2911/44	Stotzing	47.8964, 16.5310	315
B8	Sulzberghöhle	Cave, 2911/33	Stotzing	47.8970, 16.5308	310
B9	Gliridenhöhle	Cave, 2911/34	Stotzing	47.8966, 16.5310	315
U1	Tunnel no. 3	Rock tunnel, 1617/-	Ebensee	47.7856, 13.7619	475
U2	Tunnel no. 5 (Memorial site)	Rock tunnel, 1617/-	Ebensee	47.7854, 13.7615	475
S1	Grotte	Cave, 2763/2	Oberweg	47.1618, 14.6435	900
S2	Bärenhöhle im Hartelsgraben	Cave, 1714/1	Johnsbach	47.5657, 14.7101	1325
C1	Griffener Tropfsteinhöhle	Cave (show cave), 2751/1	Griffen	46.7045, 14.7313	485
T1	Tunnel at Kaiseraufstieg	Artificial tunnel, 1312/-	Ebbs	47.5934, 12.1917	605
T2	Small cleft cave no. 1	Cave, 1312/-	Ebbs	47.5935, 12.1918	610
T3	Small cleft cave no. 2	Cave, 1312/-	Ebbs	47.5931, 12.1959	650
T4	Tischoferhöhle	Cave, 1312/1	Ebbs	47.5929, 12.1970	605
T5	Shelter 1 in Kundl Gorge	Cave, 1413/-	Kundl	47.4598, 11.9904	680
T6	Shelter 2 in Kundl Gorge	Cave, 1413/-	Kundl	47.4489, 11.9842	670
T7	Small cave in Kundl Gorge	Cave, 1413/-	Wildschönau	47.4445, 11.9898	645
T8	Shelter 3 in Kundl Gorge	Cave, 1413/-	Wildschönau	47.4441, 11.9899	665

For convenience, any butterfly or moth observed in a cave is referred to as a cave lepidopteran, irrespective of its relationship to underground habitats. In order to distinguish random vagrants from more regular cave visitors it was assumed that repeated observations in domestic caves and the availability of records from foreign caves indicate a more-than-random relationship with this habitat. Three types of nonrandom cave use were distinguished: "Overwintering" lepidopterans move into caves from late summer on to spend there a period of dormancy until next springtime. "Deep diurnal retreat" pertains to species that were observed also in deeper parts of the cave and did tolerate some disturbance before they flew up. "Shallow diurnal retreat" pertains to species that were observed in the entrance zone and were more sensitive to disturbance (e.g., by the photo flash). For the distinction of the two types of daytime cave use in the warm season we analyzed the field notes with regard to resting position and behavior of lepidopterans from 471 underground sites. "Random" cave use was usually (and provisionally) attributed to species with a single subterranean record.

RESULTS

Habitat use of previously published cave-visiting Lepidoptera

In the first survey of extant cave animals of Austria, Strouhal & Vornatscher (1975) listed seven overwintering Lepidoptera. *Scoliopteryx libatrix* (55.6%), *Triphosa dubitata* (29.8%), and *Aglais io* (9.8%) made up 95% of the entries, followed by *Triphosa sabaudiata, Alucita desmodactyla*, *Hypena rostralis,* and *Aglais urticae*. Underground observations of these subtroglophile species in late summer are rather due to an early settling for winter than to mere daytime sheltering, e.g., *Alucita desmodactyla* in a Styrian cave (S1) on 07 Aug 2016 or *Hypena rostralis* in a brook tunnel in Vienna (V3) on 20 Aug 2017. Christian & Moog (1982) added six cave moths with different cave use: *Agonopterix curvipunctosa*, *Digitivalva pulicariae* and *Chloroclysta miata* (overwintering); *Camptogramma bilineata* (diurnal retreat); *Eugraphe sigma* and *Ligdia adustata* (random). Cave observations of four lepidopteran species were published by speleologists: *Harpella forficella* (Nixloch, 1665/1, Ternberg, 770 m asl: Weichenberger, 1989), *Entephria caesiata* (Wildfrauenloch, 1563/12, Gosau, 1345 m asl: Fritsch, 2008) and *Sunira circellaris* (air raid shelter Rudolfstollen, Linz, 267 m asl: Fritsch et al., 2016) exhibit random cave use, *Eupithecia undata* (Salzofenhöhle, 1624/31, Grundlsee, 2055 m asl: Kerschbaum & Pöll, 2010) has been reported from caves e.g., in Bulgaria (Guéorguiev & Beron, 1962) and might occasionally use caves for resting during daytime. Our observations after 1982 (not presented here) largely corroborate the ecological assessment of the 17 species. We only add that *Digitivalva pulicariae* appears in east Austrian caves also during the warm season. Summer and winter observations are referable to consecutive generations of this micro-moth, as reported from caves in Romania (Căpuşe & Georgescu, 1962).

First records in Austrian caves

Nineteen of the 45 newly recorded cave moth species have previously been reported from foreign caves. *Chloroclysta siterata*, *Alucita huebneri*, and *Agonopterix heracliana* were observed both overwintering and daytime sheltering on hot summer days, the remaining lepidopterans rested in caves exclusively during daytime in the warm season. Around one third (16 species) were repeatedly encountered in Austria. By far the highest number of observations pertain to *Catocala elocata* and *Mormo maura* (Table 2).

Table 2. Moth species repeatedly encountered in Austrian caves (2015-2019).

Species	Encounters/ Locations
Catocala elocata	28/21
Mormo maura	18/11
Catocala nupta	7/6
Euplagia quadripunctaria	6/6
Peribatodes rhomboidaria	6/6
Alucita huebneri	5/5
Agonopterix heracliana	5/5
Mniotype satura	5/5
Philereme transversata	5/5
Erebia aethiops	4/4
Chloroclysta siterata	3/3
Lymantria dispar	2/2
Nudaria mundana	2/2
Parascotia fuliginaria	2/2
Hofmannophila pseudospretella	2/1
Nematopogon swammerdamella	2/1

In the following, species are arranged in the order of their first cave record in Austria. Records from foreign countries are not intended to be exhaustive.

Mormo maura (Linnaeus, 1758) Old Lady, Noctuidae. Cave records from: Croatia (Jakšić, 2017); Bulgaria (Beshkov & Langourov, 2004); Romania (Rákosy, 2004); Spain (Escolà, 1982; Pérez Fernández et al., 2012); France (Centelles Bascuas, 2015); Belgium (Turquin, 1994), England (Dacie, 1985 [in an old air raid shelter], Turquin, 1994); Italy (Fabbri, 2013; Mosconi, 2006; Sciarretta et al., 2006); Malta (Skinner & Wilson, 2009). – Austria: Freinberghöhle, 1579/1, Linz, 275 m asl, 21 June 2007 (unpublished record kindly communicated by E. Fritsch). L7 (14 Aug 2016), L21 (20 July 2017, 11 July 2019), V3 (20 Aug 2017, 05 Aug 2018, 12 July 2019, 11 Aug 2019), V5 (07 Aug 2018), V6 (07 Aug 2018, 28 Aug 2018, 31 July 2019), L3 (11 Aug 2018), L15 (07 July 2019, 08 July 2019), L36 (04 Aug 2019), L24 (05 Aug 2019), L28 (10 Aug 2019), L4 (09 Sep 2019). The moths rested motionless solitarily or in groups of up to 15, partly closely nestled with imbricate wings. – Cave use: Deep diurnal retreat.

Euplagia quadripunctaria (Poda, 1761) Jersey Tiger, Erebidae: Arctiinae. Cave records from: France (Braud & Sardet, 2013); Italy (Fabbri & Poletti, 2015); Greece (Bender, 1963). – Austria: L6 (16 July 2015), T1 (27 July 2018), T2 (27 July 2018) T4 (27 July 2018), L19 (02 Aug 2019), L29 (10 Aug 2019). – Cave use: Shallow diurnal retreat.

Catocala elocata (Esper, 1787) French Red Underwing, Erebidae. Cave records from: Bulgaria (Jakšić, 2017; Beshkov & Petrov, 1996; Gueorguiev & Beron, 1962; Beron, 1994); Italy (Malavasi, 2005); Spain (Calle, 1982). – Austria: B2 (02 Aug 2015, 12 July 2018), L18 (07 July 2018, 31 July 2018, 07 Aug 2018), L17 (07 July 2018), B5 (12 July 2018), V3 (04 Aug 2018, 05 Aug 2018), B8 (09 Aug 2018), B6 (09 Aug 2018), B7 (09 Aug 2018), L21 (10 Aug 2018), L1 (11 Aug 2018), L2 (11 Aug 2018), L3 (11 Aug 2018, 31 July 2019), L24 (11 Aug 2018), L9 (18 Aug 2018), L35 (04 Aug 2019), L36 (04 Aug 2019), L25 (10 Aug 2019), B8 (24 Aug 2019), B9 (24 Aug 2019), B2 (28 July 2019), L4 (30 Aug 2019, 02 Sep 2019, 04 Sep 2019). – Cave use: Shallow diurnal retreat.

Chloroclysta siterata (Hufnagel, 1767) Red-green Carpet, Geometridae. Cave records from: Italy (Mosconi, 2011). Ebert (2001) assumed overwintering in the vegetation, because no winter observations in caves, cellars or tree holes were known. Meanwhile a cave record from Germany is available (Swabian Alb, 17 Feb 2013: Schön, 2020). – Austria: An underground record on 4 Apr 2019 suggests that *C. siterata* uses Austrian caves also for overwintering. – V3 (20 Aug 2017), L20 (4 Apr 2019), L30 (18 Aug 2019: 5 specimens). Cave use: Overwintering and deep diurnal retreat.

Alucita huebneri Wallengren, 1859, Alucitidae. Cave records from: Italy (Mosconi, 2011), Greece (Beshkov & Wegner, 2004), France and Romania (Turquin, 1994), Romania (Rákosy, 2004). – Austria: All specimens were determined by P. Buchner, partly by genital preparation. The observation in early August indicates diurnal retreat. – L21 (29 Sept 2017), B1 (19 Oct 2017: 3 specimens), V4 (25 Dec 2017), L20 (5 Oct 2018), L24 (5 Aug 2019: 3 specimens). Cave use: Overwintering and deep diurnal retreat.

Agonopterix heracliana (Linnaeus, 1758), Elachistidae. Cave records from: Czech republic (overwintering in military bunkers: Dvořák, 2000, 2002); Germany (Dobat, 1978); France (Turquin, 1994); Belgium (Dethier & Depasse, 2004). – Austria: L23 (16 Oct 2017); L34, L35, L36, L37 (4. Aug. 2019: several specimens in each object). Cave use: Overwintering and deep diurnal retreat.

Telechrysis tripuncta (Haworth, 1828) Treble-spot Tubic, Elachistidae. Cave records from: no data. – Austria: L8 (20 May 2018). The three specimens from L8 were the first record of this species for Lower Austria (*teste* P. Huemer). Lepiforum contains a record from a small cave in the Weizklamm gorge, Styria, 13 June 2020, posted by H. Pichler. Cave use: Shallow diurnal retreat.

Amphipyra pyramidea (Linnaeus, 1758) Copper Underwing, Noctuidae: Amphipyrinae. Cave records from: Italy (Lopez, 1997; Mosconi, 2011); Croatia (Kučinič, 2002); England, in cellars (Young, 1997). – Austria: L14 (21 June 2018). Cave use: Shallow diurnal retreat.

Eccopisa effractella Zeller, 1848, Pyralidae. Cave records from: no data. – Austria: L5 (22 June 2018). The specimen was determined by means of microscopic and molecular methods (P. Buchner). Cave use: Random.

Hofmannophila pseudospretella (Stainton, 1849) Brown House Moth, Oecophoridae. Cave records from: Belgium (Dethier & Depasse, 2004); Luxembourg (Werno et al., 2013); France (Lepesme, 1937); England (Macdonald, 1992). Also from Australia (Dew, 1963). – Austria: L24 (2 July 2018, 12 Aug 2018), det. P. Buchner. Each of the two specimens rested at least 20 m behind the cave entrance. Cave use: Deep diurnal retreat.

Naenia typica (Linnaeus, 1758) The Gothic, Noctuidae: Noctuinae. Cave records from: Germany, in a railway underpass (Hofsäß, n.d.). – Austria: L23 (3 July 2018). Cave use: Deep diurnal retreat.

Lymantria dispar (Linnaeus, 1758) Gypsy Moth, Erebidae: Lymantriinae. Cave records from: no data. – Austria: B2 (12 July 2018), B3 (12 July 2018). Cave use: Shallow diurnal retreat.

Horisme corticata (Treitschke, 1835), Geometridae. Cave records from: no data. – Austria: B2 (12 July 2018). Cave use: Random.

Philereme transversata (Hufnagel, 1767) Dark Umber, Geometridae. Cave records from: no data. – Austria: B2 (12 July 2018), L3 (16 June 2019), L20 (21 June 2019), L21 (23 June 2019), B8 (29 July 2019). Cave use: Deep diurnal retreat.

Phragmatobia fuliginosa (Linnaeus, 1758) Ruby Tiger, Erebidae: Arctiinae. Cave records from: no data. Austria: L31 (21 July 2018, photo record K. Bürger). Cave use: Random.

Erebia aethiops (Esper, 1777) Scotch Argus, Nymphalidae. Cave records from: no data. According to Slamova et al. (2011), the butterflies nectar in the morning and spend the hottest daytime in the shade. – Austria: T3 (27 July 2018), T4 (27 July 2018), T7 (24 July 2019), T8 (24 July 2019). Cave use: Shallow diurnal retreat.

Peribatodes rhomboidaria (Denis & Schiffermüller, 1775) Willow Beauty, Geometridae. Cave records from: no data. – Austria: V3 (4 Aug 2018), B8 (9 Aug 2018), L11 (20 Aug 2018), L10 (18 Sep 2018), L16 (10 June 2019), B3 (6 July 2019). Cave use: Shallow diurnal retreat.

Polygonia c-album (Linnaeus, 1758) Comma, Nymphalidae. Cave records from: no data. Wiklund & Tullberg (2004) and Dvořák et al. (2009) agree that *P. c-album* does not overwinter in underground shelters. – Austria: B9 (9 Aug 2018, hottest day of the year). Cave use: Random.

Yponomeuta cf. ***cagnagella / sedella***, Yponomeutidae. No reliable determination possible (the specimen was only photographed). – Austria: L3 (11 Aug 2018). Cave use: Random.

Eupithecia tripunctaria Herrich-Schäffer, 1852 White-spotted Pug, Geometridae. Cave records from: no data. – Austria: L3 (11 Aug 2018). Cave use: Random.

Timandra comae Schmidt, 1931 Blood Vein, Geometridae. Cave records from: Bulgaria (Jakšić, 2017). – Austria: L3 (11 August 2018). Cave use: Shallow diurnal retreat.

Borkhausenia fuscescens (Haworth, 1828) Small Dingy Tubic, Oecophoridae. Cave records from: no data. – Austria: L24 (12 Aug 2018), det. P. Buchner. Cave use: Random.

Mniotype satura (Denis & Schiffermüller, 1775) Beautiful Arches, Noctuidae: Xyleninae. Cave records from: no data. – Austria: U1 (23 Aug 2018), U2 (23Aug 2018), C1 (19 Sep 2018: photo record M. Kropf); T6 (24 July 2019), B2 (28 July 2019). Cave use: Deep diurnal retreat.

Epinotia tenerana (Denis & Schiffermüller, 1775) Nut Bud Moth, Tortricidae. Cave records from: no data. – Austria: U1 (23 Aug 2018). Cave use: Random (seeking rain shelter on that wet day?).

Phigalia pilosaria (Denis & Schiffermüller, 1775) Pale Brindled Beauty, Geometridae. Cave records from: no data. – Austria: B8 (26 Apr 2019). Cave use: Random.

Adela reaumurella (Linnaeus, 1758) Green Longhorn, Adelidae. Cave records from: Belgium (Dethier & Depasse, 2004). – Austria: B8 (26 Apr 2019). Cave use: Deep diurnal retreat.

Nematopogon swammerdamella (Linnaeus, 1758) Large Longhorn, Adelidae. Cave records from: no data. – Austria: B8 (26 Apr 2019, 29 July 2019). Cave use: Deep diurnal retreat.

Ectropis crepuscularia (Denis & Schiffermüller, 1775) Engrailed, Geometridae. Cave records from: Russia (Mukhanov & Kapralov, 2010). – Austria: B8 (26 Apr 2019). Cave use: Deep diurnal retreat.

Idaea aversata (Linnaeus, 1758) Riband Wave, Geometridae. Cave records from: no data. – Austria: L3 (16 June 2019). Cave use: Random.

Idaea dimidiata (Hufnagel, 1767) Single-dotted Wave, Geometridae. Cave records from: no data. – Austria: L3 (16 June 2019). Cave use: Random.

Paratalanta hyalinalis (Hübner, 1796), Crambidae. Cave records from: no data. – Austria: L3 (16 June 2019). Cave use: Random.

Aglossa pinguinalis (Linnaeus, 1758) Large Tabby Moth, Pyralidae. Cave records from: Spain (Sánchez Piñero & Pérez López, 1998); Belgium (Dethier & Depasse, 2004); Italy (Sciarretta et al., 2006; Mosconi, 2011); Romania (Rákosy, 2004; Jakšić, 2017); Greece (Beron et al., 2011). – Austria: L24 (22 June 2019). Cave use: Deep diurnal retreat.

Nudaria mundana (Linnaeus, 1761) Muslin Footman, Erebidae: Arctiinae. Cave records from: Poland (Kocot-Zalewska & Domagała, 2020); Germany (Alberti, 1938); Italy (Mosconi, 2011); France (Centelles Bascuas, 2015); Belgium (Sarlet, 1982; Dethier & Depasse, 2004). Alberti (1938) reports on the "hasty refuge" of *N. mundana* moths into rock niches and caves during thunderstorms in Germany. Italian studies refer to this species as locally eutroglophile, because it can complete the full developmental cycle inside a cave (Zilli, 1992; Sciarretta et al., 2006). According to Dethier & Depasse (2004), *N. mundana* is "sans doute le papillon le plus troglophile de notre faune". – Austria: L21 (23 June 2019: 2 specimens), L22 (23 June 2019: 5 specimens). Cave use (in Austria): Shallow diurnal retreat.

Diplodoma laichartingella (Goeze, 1783) Dotted-margin Bagworm, Psychidae. Cave records from: Luxembourg (Werno et al., 2013). – Austria: L21 (23 June 2019), det. P. Buchner, posted on Lepiforum. Cave use: Deep diurnal retreat.

Parascotia fuliginaria (Linnaeus, 1761) Waved Black, Erebidae: Boletobiinae. Cave records from: no data. – Austria: V3 (12 July 2019), L31 (21 July 2019, photo record K. Bürger). Cave use: Deep diurnal retreat.

Stauropus fagi (Linnaeus, 1758) Lobster Moth, Notodontidae. Cave records from: no data. – Austria: L31 (21 July 2019, photo record K. Bürger). Cave use: Random.

Lymantria monacha (Linnaeus, 1758) Black Arches, Erebidae: Lymantriinae. Cave records from: no data. – Austria: L31 (21 July 2019, photo record K. Bürger). Cave use: Random.

cf. ***Deileptenia ribeata*** (Clerck, 1759) Satin Beauty, Geometridae. Cave records from: no data. – Austria: T2 (24 July 2019). Cave use: Random.

Erebia ligea (Linnaeus, 1758) Arran Brown, Nymphalidae. Cave records from: no data. – Austria: T4 (24 July 2019). Cave use: Random.

Nymphalis antiopa (Linnaeus, 1758) Mourning Cloak, Nymphalidae. Cave records from: Hungary (Fazekas, 2001). – Austria: We discovered a pupa in the entrance of Tischoferhöhle: T4 (24 July 2019), det. P. Buchner. Cave use: Random.

Lasiommata maera/petropolitana, Nymphalidae. Reliable determination from the photographs is not possible. Cave records from: no data. – Austria: T7 (24 July 2019). Cave use: Random.

Catocala nupta (Linnaeus, 1767) Red Underwing, Erebidae. Cave records from: Serbia (Jakšić, 2017). – Austria: L12 (28 July 2019), L13 (28 July 2019), B8 (28 July 2019, 24 Aug 2019), L25 (10 Aug 2019), L26 (10 Aug 2019), L27 (10 Aug 2019). Cave use: Shallow diurnal retreat.

Autographa gamma (Linnaeus, 1758) Silver Y, Noctuidae: Plusiinae. Cave records from: Hungary (Fazekas, 2001), Italy (Mosconi, 2011). – Austria: L33 (19 Aug 2019). Cave use: Shallow diurnal retreat.

Ecliptopera silaceata (Denis & Schiffermüller, 1775) Small Phoenix, Geometridae. Cave records from: Italy (Sciarretta et al., 2006; Mosconi, 2011). – Austria: S2 (22 Aug 2019, photo record K. Bürger). Cave use: Deep diurnal retreat.

Rheumaptera hastata (Linnaeus, 1758) Argent and Sable, Geometridae. Cave records from: no data. – Austria: S2 (22 Aug 2019, dead specimen, photo record K. Bürger). Cave use: Random.

Temporal increase in Lepidoptera species recorded from caves in Austria

The cumulative species number of Austrian cave lepidopterans shows an accelerated increase in the years 2015-2019. In the same period of time meteorologists recorded a sharp increase in the number of hot days (Fig. 1).

DISCUSSION

For many years after 1982 the present authors did not notice any new cave moth in Austria. Starting from 2015, however, unrecorded species emerged in quick succession: 2 spp. in 2015, 1 sp. in 2016, 3 spp. in 2017, 20 spp. in 2018 and 19 spp. in 2019. This steep rise after decades of stagnation, visualized in Figure 1, extended the list of Austrian cave lepidopterans to the current total of 62 species, a number comparable to the inventories of well-investigated countries such as Italy (73 spp.) or Romania (54 spp.) (Centelles Bascuas, 2015).

Almost 4100 Lepidoptera species have been registered in Austria (Huemer, 2013, and subsequent addenda). Like everywhere else, only a fraction have nonrandom relationships with caves. Imagoes of these butterflies and moths enter deep subterranean habitats (*sensu* Culver & Pipan, 2014) only exceptionally and are thus elements of the shallow subterranean fauna (Novak et al., 2012) and, in terms of the preferred places in the cave, the parietal association (Jeannel, 1926). The best-known motive

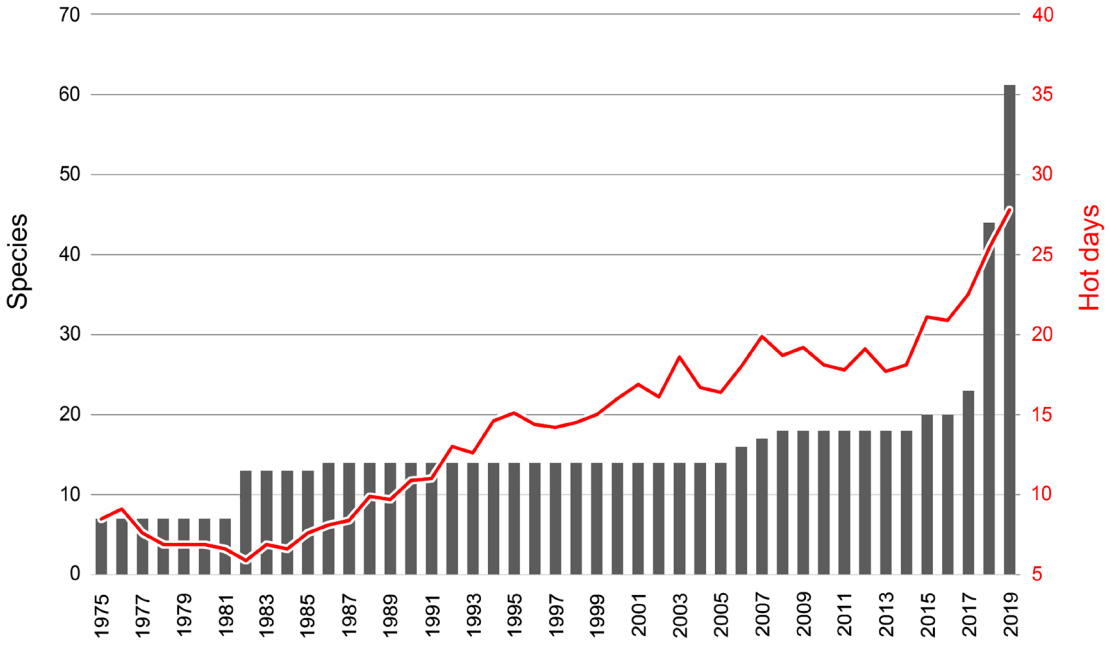

Fig. 1. Cumulative species number of Lepidoptera recorded in caves of Austria plotted against the annual number of hot days (max. ≥ 30°C, 10-year moving average). Climate data, collected at Vienna, Hohe Warte: Central Institute of Meteorology and Geodynamics.

for temporary cave residence of Lepidoptera is overwintering. Species such as *Scoliopteryx libatrix* spend a hypogean ecophase in caves or comparable locations where they remain in a dormant state, unaffected by the outer world's weather (Lipovšek et al., 2017). As would seem natural, subtroglophile species of this type first caught the attention of cavers and biospeleologists: The seven species listed by Strouhal & Vornatscher (1975) are all entering caves for overwintering. Most of the later recorded lepidopterans are either random visitors or take daytime shelter in caves on hot summer days. Among the here newly reported species, overwintering (in addition to aestival daytime retreat) has been shown only for *Chloroclysta siterata*, *Alucita huebneri* and *Agonopterix heracliana*.

Nine of the 62 Austrian cave lepidopteran species seek subterranean places for overwintering, 25 for diurnal retreat, and four display both types of cave use. 24 species are provisionally rated as random cave guests. This supports the view that the trogloxenes constitute a heterogenous cave guild (Parimuchová et al., 2018) even after the detachment of the subtroglophiles. Trogloxenes and subtroglophiles mainly occur in the twilight zone where diel and seasonal changes of environmental conditions (Mammola & Isaia, 2018) are steeply decreasing towards the interior of the cave. The differentiation of shallow and deep retreat is to account for the different behavior of lepidopterans along this gradient.

Although our inspections did not follow a rigid monitoring protocol, the rapid increase of butterfly and moth species in caves cannot be dismissed as a mere methodological artifact. Effort and diligence of data collection were virtually constant between 1978 and present, with about 80 cave inspections per year. Also during the period of increasing species numbers the frequency did not vary greatly: 89, 68, 78, and 87 inspections in the years 2015-2018, repeated visits of the same object counted. Only the 2019 peak of 147 inspections might have produced some bias – the enhanced activity was stimulated by the discoveries of the previous year. Different types of caves were inspected from the beginning of our zoological records, the proportion between natural and artificial objects did not fluctuate much. Likewise the field method remained unchanged over the time period of our analysis: We recorded all visible macrofauna at each cave inspection. The consistent procedure suggests that the recent increase in cave lepidopteran records is the reflection of a real-world phenomenon: In Austria the relations of butterflies and moths to caves have become closer.

Could the increase in cave records be a side effect of growing population density? A survey among lepidopterists revealed that this is obviously not the case. There is no indication of a local or temporal increase in relative abundance of the frequently observed cave guests during the 2010s. Therefore we favor the hypothesis that caves became more attractive diurnal resting places for a variety of butterflies and moths. And we further hypothesize that it is climate warming, particularly the increase in number and magnitude of hot days during the past years, that causes a change in the diurnal refuge preference of certain species of Lepidoptera.

Even the first newly recorded cave moth species made us think in this direction. *Euplagia quadripunctaria* and *Catocala elocata* had been known as cave guests in the southern parts of their distribution areas, in warm, mostly Mediterranean countries. As to the night and day active tiger moth *E. quadripunctaria*, evidence of cave visits in Central Europe was not available, in contrast to several published records in southern regions. The Austrian observations correspond with a French report, which says that in hot weather *E. quadripunctaria* takes refuge at various cool places including cave entrances (Braud & Sardet, 2013). The same pertains to *C. elocata* which turned out to be the most frequently encountered Austrian cave moth at mid-summer time. This species had been reported from caves in Greece, Bulgaria, Italy and Spain before. *Mormo maura* exhibits a similar pattern, albeit this species has been detected in cave-like hiding places even in England (Dacie, 1985).

Meteorological data support the hypothesis that the shift in diurnal refuge preference is climatically triggered. The five warmest summers in more than 250 years of continuous temperature recording in Austria have all occurred in the years after 2000, and summer temperatures of 2015, 2017, 2018, and 2019 were more than 3.0°C above the long-term average (ZAMG, 2019). Of particular significance in our context is the increase of hot summer days from 2015 onwards (Fig. 1). Measurements in various caves with and without moth records corroborate the assumption that many of the here reported lepidopterans are seeking cave mouths for a cool diurnal repose. We found that on hot summer days air temperature can drop by 10°C within a few meters behind the eaves line. Profiles of Sulzberghöhle (B8) may serve as an example. We determined air temperature in and around this gently declining cave with a maximum horizontal extension of 35 m in the early afternoon hours of warm days in three consecutive years. The difference between the immediate exterior and the innermost part of the cave was up to 26.6°C (Fig. 2).

Effects of climate warming on butterflies and moths have been studied from the late 1980s onwards (Kocsis & Hufnagel, 2011). Lepidoptera soon turned out to react by shifts along various axes: changes in abundance, changes in phenology, poleward and upward range expansions or shifts, and physiological and behavioral adaptations (Woiwod, 1997; Bellard et al., 2012). The responses to climate warming are largely species-specific, as shown in our data material by frequent cave records of relatively rare species. The inclination for using cave mouths as sites of diurnal repose differs even among closely related species. *C. nupta* is the most frequent *Catocala* species in Vienna and western Lower Austria, whereas *C. elocata* is rare in Vienna and absent in western Lower Austria (Schulze, 2008; Schweighofer, 2013). In terms of cave observations, however, *C. elocata* is more frequent by a factor of four.

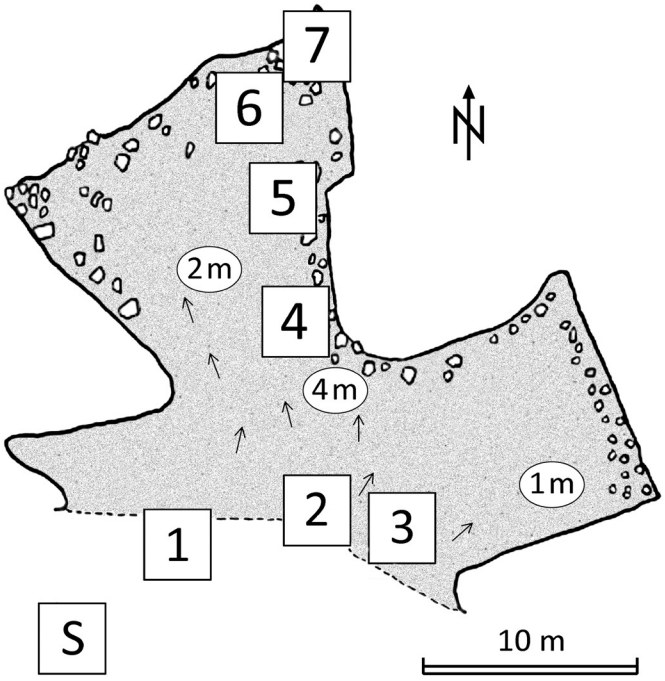

Fig. 2. Temperature transect from the surrounding deciduous forest (S) through Sulzberghöhle (Stotzing, Burgenland). Values (°C) of 09.08.2018/29.07.2019/09.08.2020. (S)..35.1/25.1/27.3, (1)..31.2/23.7/24.7, (2)..26.0/21.8/22.5, (3)..24.1/21.2/21.9, (4)..15.3/14.9/14.9, (5)..11.8/11.7/11.8, (6)..8.8/8.8/8.9, (7)..8.5/8.4/8.5.

The ascertained shift in diurnal refuge preference is most plausibly explained as a climate-induced adoption of a "southern" life style feature by Central European populations of certain Lepidoptera.

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