

## **Spring bees' activity during late summer and autumn 2018 in North Rhine-Westphalia, Germany, with some thoughts on changes of voltinism**

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### **Summary**

This paper describes the unusual phenomenon of the activity of several species of spring bees in the second half of the year well transgressing the limits of their usual season of activity by giving the most interesting facts as recorded in the state of NRW. Hypotheses on causation are presented and briefly discussed. Preliminary results were presented at the Flora-Fauna-Tag 2019 organized by the Biologische Station Westliches Ruhrgebiet BSWR.

**Keywords:** phenology, voltinism, Hymenoptera: Apoidea

### **Aktivität von Frühjahrsbienen im Spätsommer und Herbst 2018 in Nordrhein-Westfalen mit einigen Gedanken zu Veränderungen des Voltinismus**

Das ungewöhnliche Phänomen der Aktivität mehrerer Arten von Frühjahrsbienen in der zweiten Jahreshälfte deutlich außerhalb ihrer üblichen Flugzeit wird anhand der aus Nordrhein-Westfalen verfügbaren aktuellen Daten beschrieben. Denkbare Hypothesen zur Erklärung des Phänomens werden vorgestellt und knapp diskutiert. Vorläufige Ergebnisse wurden auf dem Flora-Fauna-Tag 2019, ausgerichtet von der Biologischen Station Westliches Ruhrgebiet (BSWR) vorgestellt.

**Schlüsselworte:** Phänologie, Voltinismus, Hymenoptera: Apoidea

### **Activité des abeilles printanières à la fin de l'été et à l'automne 2018 en Rhénanie-du-Nord-Westphalie avec quelques réflexions sur l'évolution du voltinisme**

Le phénomène exceptionnelle de l'activité des plusieurs espèces des abeilles sauvages printanières dans la seconde moitié de l'année, bien au-delà de leur temps de vol habituel est décrit à l'aide des données actuelles disponibles en Rhénanie-du-Nord-Westphalie. Quelques hypothèses concevable pour expliquer ce phénomène sont présentées et brièvement discutées. Les résultats préliminaires ont été présentés lors du 'Flora-Fauna-Tag' ('Journée de la Flore & Faune') 2019 organisée par la Station biologique 'Biologische Station Westliches Ruhrgebiet' (BSWR)

**Mots clés:** phénologie, voltinisme, Hyménoptères: Apoidea

## **1 Introduction**

Bartomeus et al. (2011) compared the phenological changes in a number of wild bee species with those of the flowering plants used as pollen sources by them in North America and found both to have shifted to about 10 days earlier in the last century, more or less in sync with each other. The authors interpreted this as a response to climate warming.

The occurrence of bee species (much) later than expected by their usual flight season has been noted previously but only occasionally and in (very) small numbers. Some of these records have been published. See Smit (2011, 2018) and Westrich (2018) for examples.

As the year 2018 proved exceptionally warm and dry from spring to autumn, see Schuldt et al. (2020) for an overview, we were able to observe wild bee activity well into November.

Mid-August, about the time, when the first *Colletes hederæ* males were expected to show up on *Solidago canadensis*, the first surprising finds of a univoltine solitary bee species, *Andrena cineraria*, usually active in spring only, were made more or less synchronously by several observers in the German state of North Rhine-Westphalia.

What was regarded as exceptional finds at first, caused for example by accidental unearthing of mining bee individuals by building or gardening activities, turned out to be a more pervasive phenomenon when more individuals of the same and several more species were recorded well beyond their respective normal phenologies. The first author initiated formation of a local group with several other recorders to pool all record data available for later evaluation. The spreadsheet file containing all data is available for download as supplementary material.

## 2 Observations

### 2018

Between August 8th and November 14th 2018 a total of 136 observations of spring bees of genera *Andrena* (7 species) and *Nomada* (3 species) were made by nine observers in the state of NRW. Most were made in the western part of the Ruhr area (cities of Bottrop, Dinslaken, Duisburg, Essen, Gelsenkirchen, Gladbeck, Mülheim an der Ruhr, Oberhausen) with some further north (Dorsten), south (Solingen, Haan), west (Kamp-Lintfort) and southwest (Bonn, Mönchengladbach).

Tab. 1: Number of observed animals in 2018

No.	genus species	n ind.	n ♂	n ♀	n ♀ collecting pollen
1	<i>Andrena chrysoseles</i>	8	3	5	1
2	<i>Andrena cineraria</i>	13	6	7	-
3	<i>Andrena flavipes</i> *	60	19	41	15
4	<i>Andrena haemorrhoa</i>	6	1	5	5
5	<i>Andrena nitida</i>	3	1	2	-
6	<i>Andrena scotica</i>	89	27	62	20
7	<i>Andrena tibialis</i>	2	-	2	-
8	<i>Nomada alboguttata</i>	10	3	7**	cuckoo bee
9	<i>Nomada goodeniana</i>	1	1	-	cuckoo bee
10	<i>Nomada ruficornis</i>	1	1	-	cuckoo bee

\*bivoltine species \*\* searching for host nests



Fig. 1: *Andrena cineraria* female. The illustrated individual was observed taking nectar from *Calluna vulgaris* flowers before the image was taken. | *Andrena cineraria* Weibchen. Das abgebildete Tier hatte zuvor an Besenheide *Calluna vulgaris* Nektar aufgenommen. Solingen, Ohligser Heide, 12.08.2018. Foto: Hans-Jürgen Martin



Fig. 2. *Andrena cineraria* male nectaring on Goldenrod *Solidago canadensis*. | *Andrena cineraria* Männchen, Oberhausen, 10.08.2018 beim Besuch von Kanadischer Goldrute *Solidago canadensis* in einem Garten. Foto: Bernhard Jacobi



Fig. 3: *Andrena chrysosceles* female nectaring on ivy *Hedera helix*. | *Andrena chrysosceles* Weibchen bei der Nektaraufnahme an Efeu *Hedera helix*. Mönchengladbach, 08.10.2018. Foto: Wilfried van de Sand



Fig. 4: *Andrena tibialis* female nectaring on ivy *Hedera helix*. | *Andrena tibialis* Weibchen beim Blütenbesuch an Efeu, *Hedera helix*. Duisburg, 06.10.2018. Foto: Bernhard Jacobi



Fig. 5: *Andrena nitida* female nectaring on *Tripleurospermum inodorum*. | *Andrena nitida* Weibchen bei der Nektaraufnahme an Geruchloser Strandkamille *Tripleurospermum inodorum*. Dinslaken, Emschermündung, 13.10.2018. Foto: Wilfried van de Sand.



Fig. 6: *Andrena nitida* male nectaring on *Sinapis arvensis*. | *Andrena nitida* Männchen beim Besuch von Acker-Senf *Sinapis arvensis*. Gelsenkirchen-Buer, 04.10.2018. Foto: Ingo Koslowski



Fig. 7: *Andrena scotica* female collecting pollen on ivy *Hedera helix*. | *Andrena scotica* Weibchen Pollen sammelnd an Efeu *Hedera helix*. Duisburg-Meiderich, 14.09.2018. Foto: Bernhard Jacobi



Fig. 8: *Andrena scotica* female collecting pollen on *Salix triandra*. | *Andrena scotica* Weibchen Pollen sammelnd auf Immerblühender Mandelweide *Salix triandra* 'Semperflorens'. Bottrop Kirchhellen, 28.08.2018. Foto: Volker Fockenberg



Fig. 9. + 10: *Andrena scotica* female resp. male nectaring on bryony *Bryonia dioica*. | *Andrena scotica* Weibchen bzw. Männchen Nektar aufnehmend an Rotbeeriger Zaunrübe *Bryonia dioica*. Oberhausen, 22.08.2018. Fotos: Bernhard Jacobi



Fig. 11: *Andrena haemorrhoa* female collecting pollen on *Reseda lutea*. | *Andrena haemorrhoa* Weibchen Pollen sammelnd an Gelber Resede *Reseda lutea*. Oberhausen, 23.08.2018. Foto: Bernhard Jacobi



Fig. 12: *Andrena flavipes* mating on sunflower *Helianthus giganteus*. Note the female already has been collecting pollen (repeated copulation?). | *Andrena flavipes* ♀♂ Kopulation auf Riesen-Sonnenblume *Helianthus giganteus*. Bemerkenswert ist, dass das Weibchen schon Pollen gesammelt hat (Zweitkopulation?). Oberhausen, 23.09.2018. Foto: Bernhard Jacobi





Fig. 13: *Andrena flavipes* female nectaring on dandelion *Taraxacum officinale*. | *Andrena flavipes* Weibchen Nektar aufnehmend auf Löwenzahn *Taraxacum officinale*. Oberhausen, 02.11.2018. Foto: Bernhard Jacobi



Fig. 14: *Andrena flavipes* male, resting on *Senecio inaequidens* flower head. Note mint condition of wing margins! | *Andrena flavipes* Männchen, auf Köpfchen von Ungleichzähigem Greiskraut *Senecio inaequidens* sitzend. Man beachte den frischen Zustand des Tieres, u. a. die unbeschädigten Flügelränder. Oberhausen, 08.11.2018. Foto: Bernhard Jacobi



Fig. 15. + 16: *Nomada alboguttata* female resp. male resting on sand on a springtime nesting site of host *Andrena barbilabris*. None of the latter were observed during the study (August through November). | *Nomada alboguttata* Weibchen bzw. Männchen auf Sand sitzend. An der Stelle befindet sich im Frühjahr eine Nestaggregation der Wirtsart *Andrena barbilabris*, die während der Untersuchungszeitraumes (Monate 8 bis 11) nicht gefunden wurde. Oberhausen, 09. bzw. 10.10.2018. Fotos: Bernhard Jacobi



Fig. 17: *Nomada goodeniana* male nectaring on *Helenium autumnale*. | *Nomada goodeniana* Männchen Nektar aufnehmend von Herbstalant *Helenium autumnale*. Solingen Ohligs, 23.08.2018. Foto: Hans-Jürgen Martin



Fig. 18: *Nomada ruficornis* male nectaring on Goldenrod *Solidago canadensis*. | *Nomada ruficornis* Männchen auf Kanadischer Goldrute *Solidago canadensis* Nektar aufnehmen. Gelsenkirchen-Heßler, 06.10.2018, Foto: Ingo Koslowski

### Situation in the following years (2019–2022)

In the next year (2019) the summer was very hot and dry for weeks, too, but the rains started much earlier than in 2018. Well supplied with water, *Senecio inaequidens* was flowering at least as massively as in 2018 but only a single late female *A. flavipes*, a male *cineraria*, a male *scotica* and a female *synadelpha* were found by the authors. In the following years the situation was similar, only a few individuals of 'out of season'-mining bees, again predominantly *A. scotica*, were recorded, likely representing the 'noise level'.

It must be mentioned, that during the range expansion of the Ivy bee *Colletes hederæ*, hymenopterists (including the authors) have spent quite some time inspecting flowering ivy stands to document the progress the said species made from year to year. This must have raised the chances of detecting any out-of-season spring *Andrena* individuals, that otherwise would probably have been recorded less frequently. The first *Colletes hederæ* were recorded in the area covered by this report in 2013 and searches at flowering ivy were done from 2010 on, not to miss the appearance of the expected species. Thus any *Andrena* present would have stood a good chance to be detected even given the similarity between *Andrena scotica* and the omnipresent honeybee workers.

## 3 Discussion

### Situation in neighbouring countries: Belgium and The Netherlands

A survey for 'out of the regular'-records of *Andrena scotica* on <https://waarnemingen.be/> (last viewed 2022.11.16) for Belgium (years 2010 through 2022, months August, September, October and November) produced an increase from single or zero records to 41 in 2018, while there were none in the same months of the previous decade. In the next four years (2019 through 2022) numbers of *Andrena scotica* individuals recorded in Belgium did not reach the level of 2018 but were consistently higher than in years prior to 2018 (Fig. 19).

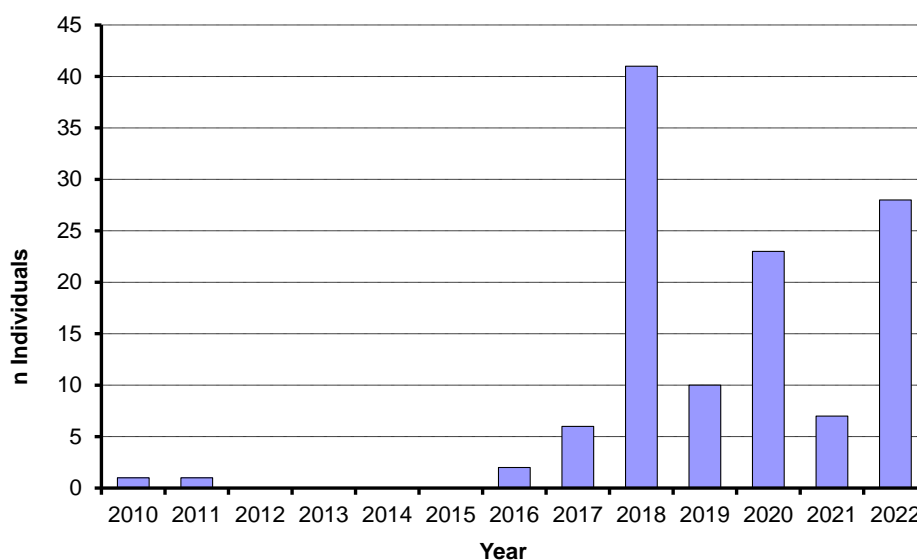


Fig. 19: Observations of *Andrena scotica* in the months of August to November in Belgium (Data from <https://waarnemingen.be/>, last viewed 11/16/2022)

A similar survey for 'out of the regular'-records of *Andrena scotica* on <https://waarneming.nl/> for the Netherlands (years 2010 through 2022, months August, September, October and November) produced an increase from zero records to 3 in 2017, peaking at 37 in 2018. The situation from 2019 through 2022 closely matches that in Belgium (Fig. 20).

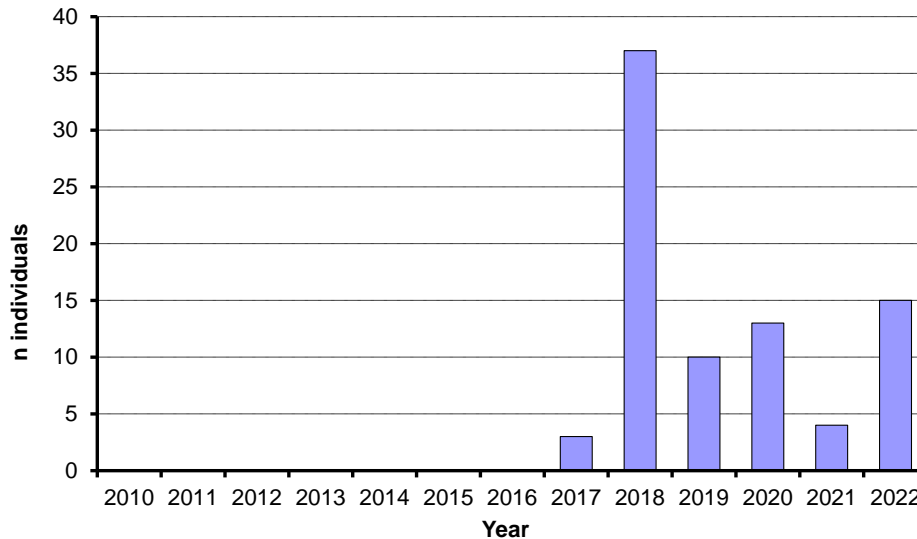


Fig. 20: Observations of *Andrena scotica* in the months of August to November in Netherlands (Data from <https://waarneming.nl>, last viewed 11/16/2022)

It is likely the phenomenon described here and also observed in Belgium and the Netherlands has occurred in other middle European countries, too.

Sadly <https://observation.org/> has but very few records of out-of-season *Andrena scotica*. As an example there are no records for Germany from 2010 through 2021. For 2022 there are only 4 records, one of which shows a honeybee worker *Apis mellifera*!

#### How do the *Andrena* species observed hibernate?

Gebhard & Röhr (1987) excavated nests of *Andrena cineraria* in October and found only fully developed adults of the species and also of their cuckoo bee *Nomada lathburiana*. So obviously *A. cineraria* hibernates as adults in their natal brood cells. So a much earlier report by Bradley (1894) on a male specimen unearthed by earthworks on a railway embankment is backed.

We were unable to retrieve information on the hibernation of the other 6 observed *Andrena* species. We by analogy assume they are spending the winter fully metamorphosed in their brood cells, too.

#### On the use of the terms 'generation' and 'brood'

**Generation** is used here in the strict sense, meaning **reproducing offspring** produced by a population of parents more or less synchronously.

**Brood** is here understood to include **any offspring** (not necessarily reproductives) of a population of parents produced more or less synchronously. Successive broods of the same female may or may not consist of workers but in any case share the same mother, so do not represent different generations. In eusocial species with long lived queen females (*Lasioglossum marginatum*) successive broods can

be produced over several years. The next generation (s. str.) in eusocial bees exclusively consists of the young reproductive individuals finally produced.<sup>1</sup>

From many observations by many observers in temperate parts of Europe we are quite sure, which of our common native bees regularly have two generations in a calendar year (*Andrena flavipes*, *Osmia caerulescens*) and which only one (*Andrena fulva*, *Osmia cornuta*).

### **Second generation available 'on demand'? *Andrena haemorrhoa* and *A. scotica***

In the literature it has been documented that both species occasionally are encountered in late summer/autumn:

For Graz (Austria) Teppner et al. (2016) states: "*A. haemorrhoa* is very abundant in spring. In September it is very rare and was observed on *Hedera* (Teppner et al. 2009: 199) and *Rhus chinensis* ♂; in 2014 females and males were observed on *R. chinensis* ♂ and ♀ several times. Thus it seems to be normal that few individuals emerge in fall" (p. 26).

For UK Else & Edwards (2018) state:

- (on *Andrena haemorrhoa*): "Univoltine with a long flight period. It is generally found from March to June with a peak, in southern Britain, in April and early May. Females are sometimes found in July, exceptionally early August" (p. 566).
- (on *Andrena tibialis*): "There is a form in central Europe that is regularly bivoltine, flying in April and May, and later from July to early August (Kocourek 1966)".
- (on *Andrena scotica*): "Presumed to be univoltine, with a prolonged period of activity, from end of March or early April to mid July. However, in Devon a freshly emerged male and female have been collected in late June, a female in mid July and another in August; these may represent a second brood. In September and early October 1989 (at the end of a particularly dry summer) several females were observed visiting *Colchicum autumnale* in a west Cornwall garden (E. C. M. Haes, pers. comm.); these females either belonged to a second brood or were very precocious individuals of the first brood of the following year" (p. 603)<sup>2</sup>.

Both species were seen by us in spring 2018 in 'normal' numbers. Not knowing in advance how climatic conditions would develop, no counts were made, though.

Premature activity of more than just the 'normal' very few offspring destined for the regular spring generation, that were already resting fully metamorphosed in their brood cells seems one possibility. But only if they had succeeded leaving offspring, a partial second generation would have entered the stage.

A second less likely possibility would be the existence of a percentage of individuals able to stay underground for two hibernations. R. Paxton (pers. comm.) did not notice any such individuals when digging up nests of this species. This strategy could fail if the soil becomes too dry and warm for too

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<sup>1</sup> Note: some cited authors use the terms differently, sometimes even synonymous

<sup>2</sup> In this citation the given 'alternatives' are identical (brood = generation in solitary/communal species). It has to be remembered that beginning and end of calendar year were defined by man and are of value in the temperate parts of the northern hemisphere, as it is the time with neither agricultural chores nor bee activity (so far!).

long a period, with starvation/desiccation threatening. In this case emergence in autumn would be a 'last chance'.

### **Postponing the second generation or adding a third generation? *Andrena flavipes***

Caution has to be applied in the case of *Andrena flavipes* which is bivoltine under normal circumstances. Because of the extreme and prolonged summer drought in 2018, more individuals than usual might have had their emergence extremely delayed, so that the number of individuals active in the months of June to August was lower than usual. A greater proportion of individuals could have emerged only after the first rainfalls had moistened the soil and at the same time caused plants within the very broad spectrum of pollen sources of the species (like *Senecio inaequidens*) to flower profusely.

This seems quite likely. We noticed the presence of 2nd generation individuals of *A. flavipes* from June to August but had the distinct impression there were fewer than usual, though we have no data to prove it.

### **Increased response to deviant climatic conditions in recently radiating species?**

Interestingly, the species most frequently encountered in the unusually dry summer weather extending well into autumn, *Andrena scotica* and *A. cineraria* were among those found poorly resolved in DNA-barcoding studies by Magnacca & Brown (2012) and Schmidt et al. (2015). The authors suggested imminent speciation tendencies as a possible explanation. Such notion was supported by Gueuning et al. (2020).

*Andrena cineraria* belongs to a complex of closely related species, including *A. barbareae* and *A. danuvia*. In this species-group *Andrena barbareae* is bivoltine.

Among the bumblebees the *Bombus lucorum*-complex also contains closely related, sometimes difficult to identify species/subspecies. The subspecies *B. terrestris dalmaticus* from south-eastern Europe and Turkey is bivoltine and probably for this reason is bred and marketed commercially for pollination in greenhouses. In the univoltine *Bombus terrestris audax* a tendency for autumn and winter nesting has been noticed in UK for the last three decades in southern England especially so in the greater London area, see Steltzer et al. (2010). So far similar observations on the continent are scanty (Jacobi unpub. obs.).

Speciation is likely to include changes in voltinism, which would limit gene flow between budding sibling species. As the studies both used COI, the early standard sequence in barcoding, resolution difficulties could be caused by the relatively low rate of SNP mutations in mitochondrial genes. Mitochondrial genes moreover are not subjected to recombination by sexual reproduction.

### **Why does the phenomenon predominantly involve *Andrena* species?**

*Andrena* is the bee genus with the largest number of species in Germany, 116 species being treated by Westrich (2019). The genus includes several subgenera and/or species groups the members of which are notoriously difficult to identify and cryptic species are still being discovered among these, for example by Praz et al. (2019).

### Why does the phenomenon predominantly involve univoltine polylege species?

An oligolectic species arguably would incur a greater risk of not encountering acceptable pollen sources when emerging off-season in relation to its usual floral hosts. Emergence in such species is expected to be triggered by the same environmental clues promoting growth/blossoming of the floral host, as detailed in a case study by Danforth (1999). By contrast, we observed the polylectic species *Andrena haemorrhoa* and *A. scotica* to collect pollen from flowering ivy *Hedera helix*, a source unavailable to the spring generation.

### Did the off-season mining bees successfully reproduce?

We are unable to answer this question, but at least in 6 of the 7 observed *Andrena* species both sexes were recorded. Only one actual mating was observed, though (*Andrena flavipes*, Fig.12). In 4 of 7 observed *Andrena* species between 1 to 20 females were observed collecting pollen, representing 20 to 100% of the females observed for each species. It seems reasonable to assume, these females had mated and were provisioning a nest with brood cells. The conditions were favourable for pollen collection for some weeks, so successful production of offspring is a possibility. Still it is unknown, if the larvae are able to develop on a diet of ivy pollen.

### What about the specific cuckoo bees?

All together we found 171 individuals of 7 *Andrena* species active off-season, but only 12 individuals of 3 species of *Nomada*. Two of the latter were species known to parasitize one or two of the *Andrena* species also observed: *Nomada ruficornis* is the specific cuckoo bee of *Andrena haemorrhoa*, while *Nomada goodeniana* parasitizes *Andrena cineraria* and *A. tibialis* and other large *Andrena* species. So obviously the observed *Andrena* species only had a very low percentage of their specific cuckoos joining them in their off-season emergence.

Else & Edwards (2018) state (for *Nomada goodeniana*): "Bivoltine, the first brood flying from early April to June or July, the second from early July to mid-August. The summer brood is rarely as common as the spring generation" (p. 433). Since every *Nomada* species is dependant on the presence of nesting hosts, it seems adaptive for the former to be less prone to off-season emergence. The few individuals of *Nomada* observed could have been stirred into unseasonal activity by host bees emerging from the same nest. The relatively large number of *Nomada alboguttata* encountered without a single find of its locally known host *Andrena barbilabris* remains unexplained as Witt (1992) in his monographical study found no indication of a second generation.

It must be added, though, that *N. alboguttata* sensu lato consists of a complex of so far unresolved forms, at least one of which is bivoltine:

- continental *Nomada baccata* with the bivoltine host *Andrena argentata*

while others are univoltine:

- British *N. baccata* with host *A. argentata*, which also is univoltine in UK
- continental *Nomada alboguttata* 'small' with the univoltine host *Andrena ventralis*
- *Nomada alboguttata* 'large' with the univoltine host *Andrena barbilabris*, recently also recorded in the UK, see Kirby-Lambert (2016)



Probably, like in the case of *Andrena scotica* and *A. trimmerana*, the complex including *Nomada alboguttata* represents a clade recently budding, which could be expected to involve changes in voltinism.

### **Accident or evolutionary strategy?**

Given the existence of uni- as well as bivoltine species in genus *Andrena*, even in the same subgenus (*Euandrena*, *Hoplandrena* a. o.) it may be worth looking at the phenomenon at hand from an evolutionary perspective.

How could two member species within one subgenus, necessarily derived from a single common ancestor back in time, have arrived at different ends, one species being univoltine the other bivoltine? Obviously, though frequently treated as alternatives, these two character states have to be connected by transient stages. There are examples of species, in which specific identity of both generations has long been doubted. For example in *A. bicolor*, the spring generation of which was named *A. gwynana* previously, until Westrich (2006) experimentally demonstrated their specific identity. In other such bivoltine species/species pairs, like *A. stragulata* and *A. rosae*, see Reemer et al. (2009) and Westrich (2014), or *A. spinigera* and *A. trimmerana*, being less common and less accessible to controlled rearing, neither possibility has been excluded as of today, so to treat them as one or two species still seems a matter of preference.

Species occupying intermediate states between one respectively two annual generations have been characterized in the extant literature as showing a 'partial second generation'. Frequently a dependency on favourable climatic conditions has been implied by expressions like "A partial second generation can occur in some southern districts [...]" Falk (2015, p. 154), referring to *Andrena scotica*.

As the observations from the extremely warm and exceptionally dry summer of 2018 indicate, the potential to put forth a second annual generation, might not be an exclusive faculty of notoriously bivoltine species, but could latently be present, in quite a number of those species we have grown accustomed to regarding as univoltine. The (hypothetical) threshold to trigger a second generation must certainly be higher in the latter than in the former, though.

Effects of Global warming (1.4°C already for Germany) seem to be already sufficient to surpass such a (hypothetic) threshold and trigger a partial second generation in several univoltine spring *Andrena* species.

Obviously individuals out of their usual season are at risk of perishing without leaving offspring and consequently without passing on their genes to the next generation. Among these genes there might be alleles imparting an increased readiness to leave the brood cell without hibernation. If a summer like in 2018 would prove a singular climatic aberration in the long run, the unusual partial second generation would stay an ephemeral phenological aberration. Should such long, warm and dry summers become more frequent or even a regular occurrence on the other hand, favourable genes would spread in the species' gene pool and a two-generation annual phenology could become firmly established.

### **Authors contributions**

Authors jointly contributed the bulk of the records: 111 (Kosłowski: 77, Jacobi: 34). Jacobi wrote the MS.

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Additional records were contributed by Wilfried van de Sand (Bottrop): 9, Volker Fockenberg (Bottrop-Kirchhellen) 5, Hans-Jürgen Martin (Solingen): 3, Markus Menke (Bonn): 3, Karola Winzer (Mülheim, observation.org): 2, Joop van de Sande (Haan, observation.org): 1, Fritjoff Jansen (Solingen): 1. Paul Westrich and Hans-Jürgen Martin both alerted me of an inconsistency in the use of terminology in an earlier version of the MS. Hans-Jürgen Martin improved the French summary and removed some mistakes from the English text. Robert Paxton brought to our notice the work of Gueuning et al. (2020). Thanks to all of them!

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