

POLLEN PREFERENCE, ECOLOGY AND CONSERVATION OF *ANDRENA SIMILLIMA* (HYMENOPTERA: ANDRENIDAE) IN CORNWALL

PATRICK SAUNDERS

West Looe Hill, Looe, Cornwall PL13 2HJ UK

paddy@kernowecology.co.uk

ABSTRACT

Field observations and analysis of pollen loads showed that the Buff-banded Mining Bee *Andrena simillima* F. Smith in Cornwall collected most of its pollen from knapweed *Centaurea nigra* (Asteraceae) and bramble *Rubus fruticosus* agg. (Rosaceae). Whilst *A. simillima* does not fit a simple binary definition of dietary specialism it qualifies in Cornwall as a specialist bee (or eclectic oligolege), taking pollen mainly from two unrelated plant genera. Potential drivers of this flower specialisation are reviewed. In Cornwall, knapweed is probably a critical conservation requirement. It is suggested that abundant knapweed (at least 450 flowers) is needed close to nest sites (probably within 900 m). Bramble is also important, but unlikely to be limiting as it is widespread and increasing generally in Cornwall. *Andrena simillima* was found nesting both solitarily and in aggregations. A tendency for aggregated nesting could make dense flowering knapweed a more critical requirement for this species. The Atlantic distribution suggests climate could be a very important factor in the conservation of this species and emphasises the importance of SW England as possibly 'the' European stronghold for the bee.

INTRODUCTION

Andrena simillima F. Smith has a single adult generation each year which is active in July and early August. *Andrena simillima* is a UK Red Data Book species with important populations in Cornwall (Falk, 1991).

The taxonomic status of *A. simillima* is complex and in need of a modern review using genetic sequencing. Some authors consider four distinct taxa to occur within the aggregate of *Andrena simillima sensu lato* in Europe. Warncke (1988) considers the various taxa within the group to be confined to different geographical regions; *Andrena s. simillima* (SW England, Western France across Central and Eastern Europe, *Andrena simillima bremensis* Alfken, (Benelux, Scandinavia, and Central Europe, see Le Divelec, 2021), *Andrena simillima sischkai* Warncke, (southeastern Europe to the Caucasus), *Andrena freygessneri* Alfken, (Alps, see Ebmer, 2001), and a further closely related taxon found in Morocco *Andrena niveofacies* Wood (Wood *et al.*, 2020).

Andrena simillima s.l. is listed in the Red Data Books of the Czech Republic, Germany, the Netherlands (Kemp *et al.*, 2013). Outside the the UK most records are historical specimens in collections with very few modern records of *A. simillima s.l.* For example In Belgium and the Netherlands, there is only a single 19th century specimen of *A. simillima s.l.* (Wood, per comm. 2023) and modern French records are suggested to be probably largely *A. nigriceps* (Genoud, per comm. 2023). Excluding *A. freygessneri* from the group which has a cluster of modern records in the Alps (Muller, 2018) .

The U.K. population is considered to be *A. s. simillima* which is the nominate form described from England (Woods, per comm. 2020) so is referred to as *Andrena*

simillima in this publication (Figs 1 and 2). It is found in scattered sites in England (Else & Edwards, 2018). Cornwall is one of the UK “hot-spots” with approximately 14 recent sites, most of which are coastal (French, 2020).

Given the paucity of modern European records the SW England populations of *A. simillima* is likely to be of European importance and should have very high rarity status (Rasmont *et al.*, 2013).

METHODS

Study sites

Survey sites were identified using *A. simillima* location records from the ERICA Cornish database (French, 2020), Malcolm Spooner (Spooner, 1984), Josh Baum and the Bees Wasps Ants Recording Society database (BWARS). Three sites on the north coast of Cornwall (Tintagel, Boscastle and Trevallus) and two on the south coast (Porthleven and Loe Bar) with strong populations of *A. simillima* were used for sampling (Figs 3–6). Study sites were up to about 80 km apart and consisted of areas of high-quality coastal habitats with both scrub edge and flower-rich maritime grasslands supporting a very rich bee fauna including a number of Nationally Scarce species. All the sites had other closely related *Andrena* spp. present, which are associated with late flowering Asteraceae notably the Grey-banded Mining Bee *Andrena denticulata* (Kirby), and the Black-headed Mining Bee *Andrena nigriceps* (Kirby) as well as *A. simillima*.

Pollen analysis

Pollen sampling was carried out between 2018 and 2020. Females caught either at nests or foraging were put in a clean tube, left for a short time for most of the pollen load to fall off into the tube, and then released. Sample tubes from individual bees were sent to Dr Judy Webb (Oxfordshire) for identification.

Pollen is difficult to identify to species level and was assigned to genus, tribe or family. Within individual pollen loads (or samples) flower content was estimated visually using a DAFOR scale (2018–19) or by percentage content (2020). The pollen types in individual samples were assigned to classes based on the assessment of constituents. Total constituents (2018–20) with > 9% content or those described as abundant or dominant within a sample were separated into a ‘major’ grouping. The



Fig. 1. Female Buff-Banded Mining Bee *Andrena simillima*. Pollen collecting on black knapweed.



Fig. 2. Male Buff-Banded Mining Bee *Andrena simillima*.

number of samples with named major pollen types present were calculated as a percentage of the total number of samples in 2018–20 ($n = 53$) (Fig. 7). The total numbers of samples (2018–20) with a named pollen type present as a major component were also counted per two-week foraging period (Fig. 8).

The proportion of each pollen type in each individual of the 2020 samples ($n = 34$) was computed by percentage (Saunders, 2023). Pollen types comprising $< 5\%$ of a sample were excluded from these results.

Constituents comprising $< 10\%$ of a sample (2018–20) were classified as 'minor' (Saunders, 2023). Pollen species in the range of $< 1\text{--}10\%$ (Wood & Roberts, 2018) and (Müller & Kuhlmann, 2008) of the load are excluded from comparable studies as they may have represented contamination. Flower and nest observations occurred between 2018 and 2022.

RESULTS

Foraging observations and sampling

The major pollen types in all 2018–20 samples ($n = 53$) mainly came from only two species of flowering plant (Fig. 1.) with bramble *Rubus fruticosus* agg. in 75.5% of samples and knapweed *Centaurea nigra* in 52.8%. Total pollen content of all 2020 samples ($n = 34$) consisted of 49% *Rubus fruticosus* agg. and 41% *Centaurea nigra*. This was notable considering the very high diversity of available flower resources and the diversity of 'minor' pollen types (Saunders, 2023). Fifteen per cent of samples with major components consisted of other Asteraceae, mainly thistles (*Cirsium spp.*) and, in one sample, probably goldenrod *Solidago virgaurea*.

Field observations broadly confirmed the results of the pollen sampling with 50% of recorded bees observed on *Centaurea nigra* and 35% on *Rubus fruticosus* agg. ($n = 69$ observations).

Pollen from umbellifers (Apiaceae), probably wild carrot *Daucus carota*, was also present but only as major component in 3.8% of samples, despite the plants being abundant at all sites.

In most samples one major pollen type was dominant. In the 2020 samples ($n = 34$) only three samples comprised mixtures with no one pollen type having $> 50\%$ content.

The minor constituents ($< 10\%$) of the pollen samples were much more diverse, with 15 pollen types from eight plant families compared to the major or dominant classes with seven pollen types from three plant families, suggesting a wide range of available pollen types were not being chosen by the bee, although the most frequent minor types (77%) were still various Asteraceae (Saunders, 2023). Most of this minor class were present in very small or trace quantities with only eight out of 53 samples comprising $> 4\%$. Probably most represent contamination, such as pollen transfer on the flower head by other non specialist flower visitors. For example, all the samples from Boscastle in 2019 contained trace amounts of anthemid type pollen, most likely from corn marigold (*Glebionis segetum*) which was present in superabundance in a open field strip close to the sampling area (Fig. 6).

Nesting in Cornwall

Nests of *A. simillima* were found at two survey sites (Boscastle and Porthleven), in silty loam soil on small areas of sloping or vertical bare ground, with a range of aspects, but predominantly south-west and north-west. Most of the nests at Boscastle



Fig. 3. An aggregation of *Andrena simillima* was observed nesting in vertical bare ground below the rough slate step of the coast-path at Boscastle, 2019.



Fig. 4. Nesting site of *Andrena simillima* in a stone wall at Porthleven, 2020.



Fig. 5. Sample site Tintagel, 2020. Species-rich maritime meadow with high diversity of flowers including umbellifers and other asters used by a range of bee species. *Andrena simillima* showed a preference for knapweed based on frequency of flower visits and pollen load analysis, despite the rich range of other flower species present.



Fig. 6. *Andrena simillima* only collected trace amounts of anthemid pollen at Boscastle in 2019, despite the large stand of corn marigold (shown) growing 100 m from the sampling site.

occurred along the heavily compacted edges of a very well used section of the South West Coast Path. Two of the Boscastle nests were adjacent to very dark slate rocks.

The 2016 Boscastle nest site had an aggregation of at least 4–6 females with a similar number of males occupying about 0.5 m² of vertical bare ground and sparsely vegetated bank (Fig. 3). A nest area found in 2019 nearby had a small aggregation of about four females. In 2019 single females were also observed nesting solitarily in close proximity to both the 2016 and 2019 nest aggregations. The nests at Porthleven, associated with an aggregation of at least 10–15 females, were in loamy soil on vertical bare ground and in gaps in stones in a west facing hedge-bank (Fig. 4).

The cleptoparasite of *A. simillima* is considered to be the Black-horned Nomad Bee (*Nomada rufipes* F.) (Westrich, 2018; Else & Edwards, 2018). In 2016 a red form of *Nomada rufipes* (in 2016 and 2019), and a dark form (in 2019,) were seen investigating the nest aggregation at Boscastle.

Flower specialisation

Andrena simillima is listed in the literature as visiting (for pollen and/or nectar) *Cirsium* sp., *Centaurea* sp., hemp agrimony *Eupatorium cannabinum*, brambles *Rubus fruticosus* agg. and wild marjoram *Origanum vulgare* (Falk, 2015) (Else & Edwards, 2018), *Hebe* (S. Poland pers. comm.) and wild carrot *Daucus carota* (Spooner, 1984). Else & Edwards (2018) observed a very strong preference for *Rubus fruticosus* agg. and *Centaurea scabiosa*. Individuals have been observed collecting pollen from flowers of common fleabane *Pulicaria dysenterica* (Edwards & Broad, 2006). Many bees take nectar from a wider range of plant species than their pollen hosts; pollen hosts are likely to be more critical than nectar hosts for species conservation (Danforth *et al.*, 2019).

Some of the factors driving pollen-host specialisation include physiological adaptations by individual bee species to digest certain pollens, foraging efficiency, phenology, quality and quantity of available flower resources and competition with other species (Danforth *et al.*, 2019). It is likely the interplay between these factors that affects foraging choices and reproductive success. Bees are usually defined as oligolectic when flower specialist or polyolectic when generalist.

The populations of *A. simillima* studied here can be classified as ‘eclectic oligoleges’ because they took the great majority of their pollen from two unrelated genera, *Centaurea* and *Rubus*, or ‘facultative oligoleges’ because they took *Rubus* pollen early in the season but switched to *Centaurea* pollen when that became available (Cane & Sipes, 2007) (Fig. 8).

The sample sites had extremely rich flower resources which was also reflected in the diversity of trace results (Fig. 5).

Centaurea sp. and *Cirsium* sp. are both in the Cynareae tribe of the Asteraceae, and share similar flower structure (Westrich, 2018). Taxonomically related plant pollens have been found to have similar amino acid content (Wiener *et al.*, 2010). All the study sites apart from Porthleven had other abundant Asteraceae, particularly saw-wort *Serratula tinctoria* and various *Cirsium* spp. flowering at the same time, but the bees mainly still chose *Centaurea nigra*. *Centaurea nigra* was much rarer than *Rubus fruticosus* agg., but was still favoured on most sites. Apiaceae including wild carrot and hogweed *Heracleum sphondylium* were as abundant as bramble at most sites, but rarely used.

Pollen load samples collected from bees at the Porthleven nest (n = 13) consisted of very little other than bramble pollen. Despite knapweed being very rare within 800 m, two Porthleven samples had >40% *Centaurea nigra* pollen content. Yellow asters were

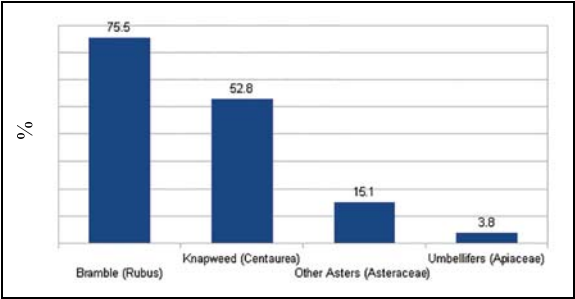


Fig. 7. Percentage of total *Andrena simillima* samples with a named major pollen component. Pollen types were classified as major when having either >9% content (2020) or when recorded as abundant or dominant (2018–19) (n = 53). Other Asteraceae were mostly thistles (*Cirsium*) or other Cynareae and the Apiaceae were likely to be wild carrot (*Daucus carota*).

very abundant near this nest but only one sample had *Lactuceae* type and only at 9% content, whereas four Porthleven samples had >9% *Cirsium* pollen which was occasional in the vicinity. *Daucus carota* pollen was not found in any of these samples despite the plant being very abundant nearby.

A literature review found mixed evidence that either *Centaurea* sp. or *Rubus* spp. were better quality pollen resources than other wildflowers. *Centaurea nigra* has high mean pollen volume (Hicks *et al.*, 2016). *Centaurea scabiosa* had the highest pollen yield of any ruderal wildflowers (Denisow, 2011). *Rubus fruticosus* agg. has higher essential amino acid content than *Centaurea* (Wiener *et al.*, 2010). *Rubus fruticosus* agg. and *Centaurea nigra* are similar in protein lipid ratio and roughly average in the nutritional value of common flower species studied (Vaudo *et al.*, 2020). Pollen sterol content also could be important for bees (Vanderplanck *et al.*, 2020b) but comparisons could not be made for these two species.

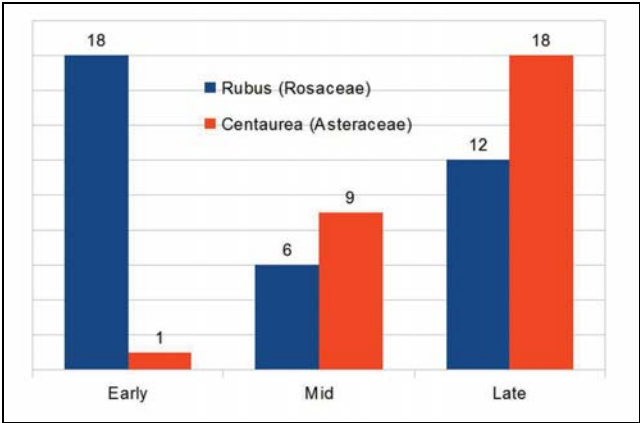


Fig. 8. Numbers of *Andrena simillima* with major pollen content loads, per two-week period starting 1st July (2018–20).

Some authors discuss the “Asteraceae paradox”, with bees said to “either use it or avoid it”, as it is deficient in some amino acids and difficult to digest (Praz *et al.*, 2008). Generalist bumblebees avoid Asteraceae probably due to their chemical defences (Vanderplanck *et al.*, 2020a). There are a large number of Asteraceae specialist bees whereas Rosaceae is thought to mainly support unspecialised bees with only two central European Rosaceae specialists known, neither *Rubus* specialists (Westrich, 2018).

Andrenidae have very high rates of species diversity in Europe and it is thought closely related species may co-exist by fine tuning their phenology to exploit a narrow range of flower species within the same host plant family (McLaughlin *et al.*, 2022). Aster preference is found within the close relatives of *A. simillima*. *A. denticulata* and *A. tridentata* (Kemp *et al.*, 2013) are considered Asteraceae specialists and *A. nigriceps* has a strong association with asters. In Europe *A. simillima* ssp. *bremensis* preferred to visit *Jasione montana* (Van der Smissen, J., 2001, quoting from Stoeckhert) and *A. simillima* ssp. *sischkai* was observed on *Solidago virgaurea* (Ebmer 2001). Tansy (*Tanacetum vulgare*) could be an important resource for *A. simillima* s.l. in a German study (Mader & Vokl, 2001).

Diverse behavioural adaptations (such as “buzz foraging” and “scrabbling”) may dictate which flower niche a bee species is most effective at utilising (Portman *et al.*, 2019). In *Centaurea* sp. pollen is not released until the filaments are irritated by the visit of a pollinator (Faegri & Van der Pijl, 1979). *Andrena simillima* was observed curling its body and pushing flower tubes in a bunch. Perhaps special techniques for pollen harvesting on *Centaurea* sp. also work well on *Rubus fruticosus* agg.

The phenology of pollen resources is likely to be very important. In Cornwall flowering in *Centaurea nigra* is probably better synchronised with peak bee foraging than flowering in *Rubus fruticosus* agg. which on many sites was in decline by late July. The Agriland database (Baude *et al.*, 2016) records an earlier peak flowering date for *Rubus fruticosus* agg. (16/7) than *Centaurea nigra* (31/7).

Scrub-edge habitats in Cornwall typically have dispersed or linear flower resources over a large area (e.g. hedgerows), whereas hay-meadow habitats can have dense flower resources in compact areas. Low density but wide ranging populations with solitary nesting and unspecialised forage choice could be the most viable strategy in scrub-edge habitats, whereas hay-meadow habitats may favour denser populations with aggregated nesting and specialist diets. The latter could be a very efficient strategy for optimising pollen harvesting in high quality habitats but does risk a species being restricted to a rarer habitat. Linking these factors in this hypothesis maybe an inference too far but does warrant consideration, as in this study the closely related *Andrena nigriceps* was found in small numbers on a great range of flowers, which may make it a more successful scrub edge bee, whereas *A. simillima* which was usually found in more clustered populations thus could be more adapted to a hay-meadow niche.

How many flowers do they need?

Larsson & Franzen (2007) estimated that 780 flowers are needed to provision 10 larval cells of the Large Scabious Mining Bee *Andrena hattorfiana* (F.). To estimate the number of *Centaurea* flowers needed to provision a viable population of *A. simillima* (e.g. 150 larvae), I used the estimated pollen volume requirement of *Andrena ruficrus* (Mueller *et al.*, 2006) and daily pollen volume per compound flower (Baude *et al.*, 2016) giving a “ball park” estimate of 455 *Centaurea nigra* flower heads. This is an extremely rough minimal estimate as the levels of brood failure and

parasitism are unknown, and it takes no account of bad weather and competition by other species. It could also be modified by the amount of bramble or other flowers used.

How near the nest should the flowers be?

Quantifying optimal or maximum foraging range is very difficult for any solitary bee species and unconfirmed for this species. *Andrena simillima* has been calculated here to have a maximum foraging range of just under 700 m (based on body size with an inter tegular distance of c. 2.28 mm) using a formula by Greenleaf *et al.* (2007). One review found *Andrena* have maximum foraging distances of 300–600 m, but two species were found to forage 1000–1250 m from their nests (Zurbuchen, 2010). Franzen (2009) suggested a maximum foraging distance of 900 m for *Andrena hattorfiana* within his study area.

In Cornwall, flower-rich coastal habitats are usually linear, confined to a narrow strip bounded by poorer habitats inland, which gives greater confidence when tracking foraging activity. The study combined the sampling results from nest sites with observations along a linear transect up to about 2 km from the nests to provide some measure of estimated foraging distance. At Boscastle most observations of *Andrena simillima* were within 300 m of nest sites, but some bees were found 900 m away. At Porthleven they were using bramble flowers 200 m from the known nest site and larger numbers from unknown nest sites were foraging on *Centaurea nigra* at Loe Bar (1 km away).

True optimal (or most efficient) foraging range is very difficult to estimate but the scarcity of *Centaurea nigra* in the samples from the Porthleven nest site, despite the high abundance of *Centaurea* samples and foraging individuals at Loe Bar on the same day suggests that few or no bees were travelling 1 km to Loe Bar. A pragmatic estimate of an efficient foraging range in coastal Cornwall would therefore be about 900 m.

Nest Requirements

The study found the bee nesting both in aggregations (tight groups of individual nest holes) and solitarily (single or well spaced individual nest holes). A few *Andrena* do have communal nest entrances (Falk, 2015), this was not found and has not been suggested for this species. The distinction between solitary and aggregated nesting may not be so clear cut. On one site individual nests were observed widely spaced but in a discrete area used over at least five years. The bee is rare but on the study sites it seemed relatively numerous (and more so than the closely related *A. denticulata* and *A. nigriceps*). This suggested population density for this species was relatively high even if the bee does not always nest in aggregations.

Published information on the nesting of *A. simillima* s.l. is limited (Westrich 2018) but does broadly agree with this research and suggest there is a requirement for sheltered bare ground (in common with most *Andrena* species). There is a paucity of studies defining the micro-climatic and substrate requirements for any andrenid (Antoine & Forrest, 2021), although the European distribution in Warncke (1988) suggests the Atlantic climatic envelope could be an particularly important factor for *Andrena simillima*.

Conservation

Species-rich grassland has declined in the UK (Fuller, 1987) and pollinators associated with late flowering meadows have experienced greater declines than spring flying pollinators (Balfour, 2018). Boosting late summer flower resources may be the

most effective intervention to increase bumblebee populations on farmland (Timberlake *et al.* 2021).

In Cornwall most of the highest quality semi-natural grasslands are coastal. Whilst many are owned by conservation bodies and/or are protected sites, management can be difficult and the economic value of conservation grazing poor. This is leading to scrub encroachment on many sites, with blackthorn *Prunus spinosa* and bramble probably increasing. In Cornwall bee species associated with scrub edge (or bramble) that have increased recently include the Tree Bumblebee *Bombus hypnorum* L. and the Big-headed Mining Bee *Andrena bucephala* Stephens (French, 2020), whereas the late grassland associates Broken-belted Bumblebee *Bombus soroeensis* F., Shrill Carder Bee *Bombus sylvarum* L. (Saunders, 2016) and Small Scabious Mining Bee *Andrena marginata* F. are probably now extinct in the county (French, 2020).

The North Cornwall coast is extremely important for scarce bees because of its landscape scale connectivity of flower-rich grassland habitats (Saunders, 2016). *Centaurea nigra* in Cornwall is a rich resource for scarce bees, including the Black-headed Mining Bee *Andrena nigriceps*, the Brown Banded Carder Bumblebees *Bombus humilis* Illiger and the local Green-eyed Flower Bee *Anthophora bimaculata* (Panzer), and actions for *Andrena simillima* are likely to benefit other bee species.

ACKNOWLEDGEMENTS

Thanks to Dr. Judy Webb (Oxfordshire), John Badmin, Dr. Adrian Spalding, Josh Baum, Cerin Poland, Dr. Paul Westrich, Dr Tom Wood, Mike Edwards, National Trust Cornwall, Bees Wasps Ants Recording Society, Richard Hardy, Sarah Corbet and two anonymous referees.

REFERENCES

- Alfken, J. D. 1904. *Andrena Frey-Gessneri*, eine neue alpine Andrena-Art aus der Schweiz. *Societas entomologica* **19**: 81–82.
- Antoine, C. M. & Forrest, J. R. 2021. Nesting habitat of ground-nesting bees: a review. *Ecological Entomology* **462**: 143–159.
- Balfour, N. J., Ollerton, J., Castellanos, M. C. & Ratnieks, F. L. 2018. British phenological records indicate high diversity and extinction rates among late-summer-flying pollinators. *Biological Conservation* **222**: 278–283.
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A., & Memmott, J. 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* **530** (7588): 85–88.
- Cane, J. H. & Sipes, S. 2007. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. pp. 99–122 in Waser, N. M. & Ollerton, J. (eds) *Plant-pollinator interactions. From specialization to generalization*. University of Chicago Press, Chicago and London.
- Danforth, B. N., Minckley, R. L., Neff, J. L., & Fawcett, F. 2019. *The solitary bees: biology, evolution, conservation*. Princeton University Press.
- Denisow, B. 2011. Pollen production of selected ruderal plant species in the Lublin area. WUP Wydawnictwo Uniwersytetu Przyrodniczego.
- Divelec, R. 2021. Sur La Présence En France de Certaines Espèces d'Apoïdes (Hymenoptera, Andrenidae, Colletidae, Megachilidae, Psenidae). *Bulletin de La Société Entomologique de France* **126**: 103–22.
- Else, G. & Edwards, M. 2018. *Handbook of the Bees of the British Isles*. 2 vols. The Ray Society, London.

- Eckhardt, M., Haider, M., Dorn, S. & Müller, A. 2014. Pollen mixing in pollen generalist solitary bees: a possible strategy to complement or mitigate unfavourable pollen properties? *Journal of Animal Ecology* **83**: 588–597.
- Edwards, R. & Broad, G. eds., 2006. *Provisional atlas of the aculeate Hymenoptera of Britain and Ireland*. Part 6. Biological Records Centre. Huntingdon. Faegri, K., & Van der Pijl, L. 1979. *Principles of pollination ecology*. Pergamon Press. Oxford.
- Falk, S. 1991. *A review of the scarce and threatened bees, wasps and ants of Great Britain* (No. 35). Nature Conservancy Council for England.
- Falk, S. 2015. *Field Guide to the Bees of Great Britain and Ireland*. Bloomsbury publishing.
- Franzén, M. & Larsson, M. 2007. Pollen harvesting and reproductive rates in specialized solitary bees. In *Annales Zoologici Fennici* (pp. 405–414).
- Franzén, M., Larsson, M. & Nilsson, S. G. 2009. Small local population sizes and high habitat patch fidelity in a specialised solitary bee. *Journal of Insect Conservation* **13**: 89–95.
- French, C. 2020. ERICA for Windows Software. ERICA Camborne, <http://www.cornishbiodiversitynetwork.org/index.html>
- French, C. 2020. *A Flora of Cornwall*. Colin French (privately published.)
- Fuller, R. M. 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–1984. *Biological Conservation* **40**: 281–300.
- Greenleaf, S. S., Williams, N. M., Winfree, R. & Kremen, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* **153**: 589–596.
- Hanley, M. E., Franco, M., Pichon, S., Darvill, B. & Goulson, D. 2008. Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Functional Ecology* **22**: 592–598.
- Hicks, D. M., Ouvrard, P., Baldock, K. C., Baude, M., Goddard, M. A., Kunin, W. E., & Stone, G. N. 2016. Food for pollinators: quantifying the nectar and pollen resources of urban flower meadows. *PloS one*, 11(6), e0158117.
- Kemp, J. R., Michez, D., Nieto, A., Radchenko, V. & Roberts, S. 2013. *Andrena simillima*. The IUCN Red List of Threatened Species 2013: e.T19199114A43114609. Downloaded on 10 February 2020.
- Larkin, L. L., Neff, J. L., & Simpson, B. B. 2008. The evolution of a pollen diet: host choice and diet breadth of *Andrena* bees (Hymenoptera: Andrenidae). *Apidologie* **39**: 133–145.
- Larsson, M., & Franzén, M. 2007. Critical resource levels of pollen for the declining bee *Andrena hattorfiana* (Hymenoptera, Andrenidae). *Biological Conservation* **134**: 405–414.
- Mader, D. & Völkl, W. 2001. Wiederfund der Sandbiene *Andrena simillima*, Smith 1851 in Bayern (Hymenoptera, Apoidea). *Bericht naturforsch. Gesellschaft Bamberg* **76**: 135–136.
- McLaughlin, G., Gueuning, M., Genoud, D., Frey, J. E. & Praz, C., 2022. Why are there so many species of mining bees (Hymenoptera, Andrenidae)? The possible roles of phenology and *Wolbachia* incompatibility in maintaining species boundaries in the *Andrena proxima*-complex. *Systematic Entomology*. **48**: 127–141
- Müller, A., & Kuhlmann, M. 2008. Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biological Journal of the Linnean Society* **95**: 719–733.
- Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C. & Dorn, S. 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee–flower relationships. *Biological Conservation* **130**: 604–615.
- Müller, A. 2018. Pollen host selection by predominantly alpine bee species of the genera *Andrena*, *Panurginus*, *Dufourea*, *Megachile*, *Hoplitis* and *Osmia* (Hymenoptera, Apoidea). *Alpine Entomology*, **2**: 101–113.
- Portman, Z. M., Orr, M. C. & Griswold, T. 2019. A review and updated classification of pollen gathering behavior in bees (Hymenoptera, Apoidea). *Journal of Hymenoptera Research* **71**: 171–208.
- Praz, C. J., Müller, A. & Dorn, S. 2008. Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen? *Ecology* **89**: 795–804.
- Rasmont, P., Roberts, S. P. M., Michez, D., Schweiger, O., Franzen, M., De Meulemeester, T., Tomozei, B. & Radchenko, V. 2013. *Atlas of the European Bees: genus Andrena*. 1st

- Edition. STEP Project, Atlas Hymenoptera, Mons, Gembloux. <http://www.zoologie.umh.ac.be/hymenoptera/page.aspx?ID=243>
- Saunders, P. 2016. *Bumblebees of Cornwall and Scilly, an atlas and conservation guide*, ERCCIS, Allet.
- Saunders, P. 2023. APPENDIX <http://kernowecology.co.uk/Publications/T1%202023.pdf>
- Sedivy, C., Dorn, S., Widmer, A. & Müller, A. 2013. Host range evolution in a selected group of osmiine bees (Hymenoptera: Megachilidae): the Boraginaceae-Fabaceae paradox. *Biological Journal of the Linnean Society* **108**: 35–54.
- Spooner, G. M. S. 1984. *Cornish aculeate Hymenoptera register*. Unpublished handwritten notes held by ERCCIS, Allet.
- Timberlake, T. P., Vaughan, I. P., Baude, M. & Memmott, J. 2021. Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *Journal of Applied Ecology* **58**: 1006–1016.
- Warncke, K. 1988. Isolierte Bienenvorkommen auf dem Olymp in Griechenland (Hymenoptera, Apidae). *Linzer biologische Beiträge* **20**: 83–117.
- Westrich, P. 2018. *Die Wildbienen Deutschlands*. Ulmer.
- Weiner, C. N., Hilpert, A., Werner, M., Linsenmair, K. E. & Blüthgen, N. 2010. Pollen amino acids and flower specialisation in solitary bees. *Apidologie* **41**: 476–487.
- Wood, T. J. & Roberts, S. P. 2018. Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. *Biological Journal of the Linnean Society* **124**: 732–746.
- Vaudo, A. D., Tooker, J. F., Patch, H. M., Biddinger, D. J., Coccia, M., Crone, M. K. & Grozinger, C. M. 2020. Pollen protein: lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects* **11**: 132.
- Vanderplanck, M., Gilles, H., Nonclercq, D., Duez, P., & Gerbaux, P. 2020a. Asteraceae paradox: Chemical and mechanical protection of *Taraxacum* pollen. *Insects* **11**: 304.
- Vanderplanck, M., Zerck, P. L., Lognay, G. & Michez, D. 2020b. Generalized host-plant feeding can hide sterol-specialized foraging behaviors in bee–plant interactions. *Ecology and Evolution* **10**: 150–162.
- Zurbuchen, A., Landert, L., Klaißer, J., Müller, A., Hein, S. & Dorn, S. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation* **143**: 669–676.