OPEN ACCESS

The Formal Model for the solitary bee *Osmia bicornis* L. agent-based model

Elżbieta Ziółkowska[‡], Agnieszka J. Bednarska[‡], Ryszard Laskowski[‡], Christopher J. Topping[§]

‡ Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland
§ Social-Ecological Systems Simulation Centre, Aarhus University, Aarhus C, Denmark

Corresponding author: Elżbieta Ziółkowska (e.ziolkowska@uj.edu.pl)

Abstract

Solitary bees provide an important ecological and agricultural service by pollinating both wild plants and crops, often more effectively than honey bees. In the context of worldwide pollinators' declines, it is important to better understand the functioning of populations under multiple stressors at larger spatial and temporal scales. Here we propose building a detailed, spatially-explicit agent-based model of one of the best-studied species of solitary bees, *Osmia bicornis* L. In this Formal Model, we review various aspects of *O. bicornis* biology and ecology in detail and provide descriptions of their planned implementations in the model. We also discuss the model gaps and limitations, as well as inclusions and exclusions, allowing a dialogue with the reviewers about the model's design.

The ALMaSS model of *O. bicornis* aims to provide a realistic and detailed representation *of O. bicornis* populations in space and time in European agricultural landscapes. The model will be a part of the Animal, Landscape and Man Simulation System (ALMaSS); thus will be able to utilise a highly detailed, dynamic ALMaSS landscape model. It will consider the behaviour of all bee life stages daily and use state transitions to allow each individual to decide their behaviour. The development of egg-to-pupa stages in the nest will be temperature-driven. Adult bees, after they emerge from the nest in spring, will interact with the environment. They will be able to search for suitable nesting locations, provision their brood cells with pollen and reproduce. Modelled females will balance offspring size and

number following the optimal allocation theory, but local environmental factors will modify their actual parental investment decisions. The model will include the daily mortality rate for the egg-to-pupa stages, overwintering mortality, and background mortality outside the nest. We will also consider the risk of open-cell parasitism as increasing with the time the brood cell is open.

With the level of detail suggested, the model will be able to simulate population-level dynamics in response to multiple factors at the landscape scale over long periods. The European Food Safety Authority (EFSA) has suggested *O. bicornis* as a model organism for non-*Apis* solitary bees in the pesticide risk assessment scheme. Therefore, we hope our model will be a first step in building future landscape risk assessments for solitary bees.

Keywords

agroecosystem, pollinators, population dynamics, spatially-explicit model, wild bees

Introduction

Over the last few decades, a dramatic decrease in the abundance of arthropods has been observed worldwide, especially in agricultural landscapes (Sánchez-Bayo and Wyckhuys 2019, Seibold et al. 2019). Pollinators seem to be particularly endangered, as indicated by a rapid decline in the abundance of butterflies and bees (Potts et al. 2010, Potts et al. 2010 , Nilsson et al. 2013, Powney et al. 2019). This decline has been blamed on many factors. These include agrochemical use, intensification of agricultural practices and habitat degradation, but also parasites and pathogens, invasive species, poor nutrition and climate change (Goulson et al. 2015, Sánchez-Bayo and Wyckhuys 2019). Since these factors co-vary and interact, a broader system-based perspective is needed to unravel this complexity and determine the relative importance of each of the factors (More et al. 2021, Topping et al. 2021). A modelling approach, coupling a detailed spatiotemporal landscape model with agent-based population modelling, has been shown to be a useful tool for understanding the functioning of populations under multiple stressors at larger spatial and temporal scales (Topping et al. 2015, Ziółkowska et al. 2021, Ziółkowska et al. 2022). One of the critical groups of species necessary for this approach is the solitary bees and, of these, probably the *Osmia* genus is best understood.

Here, we present a Formal Model of a spatially-explicit agent-based model for the solitary red mason bee *Osmia bicornis* (Linnaeus, 1758, Hymenoptera: Megachilidae, formerly *Osmia rufa* L.). The description follows the "Formal Model" format proposed by Topping et al. (2022) and is the first step in the model cycle before its implementation and calibration. The model is under development within the Animal, Landscape and Man Simulation System (ALMaSS) modelling framework (Topping et al. 2003; Topping 2022). Agent-based models have previously been applied to assess aspects of the population dynamics of solitary bees. The SOLBEE model, developed by Everaars and Dormann (2014), simulates

the behaviour and movement of pollen-collecting solitary bees with different life history traits in a 1 x 1 km agricultural landscape. It incorporates details of foraging resources and tracks pollination services (number of flowers visited, foraging habitat visitation and foraging distance) within a foraging day with a time step of one second. However, it does not address the population dynamics at larger scales and population-level responses to multiple factors. On the other hand, the individual-based model of *O. bicornis* by Ulbrich and Seidelmann (2001) investigates long-term population development in response to fluctuating environmental conditions by relating maternal investment to habitat quality and the risk of parasitism. In their model, habitat quality and availability of resources are modelled in a simplified way and expressed in terms of cell construction time without considering the environmental factors affecting these.

In contrast to these existing models, our model will be the first fully spatially-explicit one to model population-level dynamics in response to multiple factors at the landscape scale (up to hundreds of km^2) over long periods (decades). The behaviour of individual bees will emerge from bees' interactions with the environment, which in ALMaSS is represented by a highly detailed, dynamic landscape model (Topping et al. 2016). The landscape model can simulate the impacts of weather, food and nesting availability and landscape management, thus impacting the bees' population dynamics. The ALMaSS model of *O. bicornis* also has the ultimate purpose of being included in a system of models for the risk assessment of pesticides, hence will also utilise ALMaSS pesticide simulation components.

In the context of worldwide declines in pollinator populations, most scientific efforts, legislation and conservation practices have focused on a single species, the western honey bee *Apis mellifera*. For many years, the USA and Europe have also focused on the honey bee for assessing environmental risks for pollinators. Recently, the European Food Safety Authority (EFSA) has promoted the development of a system-based approach to the environmental risk assessment of multiple stressors in honey bees (More et al. 2021), including the development of an agent-based honey bee colony model ApisRAM (Duan et al. 2022). Although a significant proportion of global crop pollination demands depends on managed honey bees, the role of wild bees in pollination should not be underestimated (Garibaldi et al. 2013, Willmer et al. 2017). In fact, wild bees are often more effective pollinators than honey bees (Winfree et al. 2008). In addition, they differ in their response to floral abundance and preference for different plants (Urbanowicz et al. 2020). Furthermore, due to their biological and morphological differences and lack of social lifestyle, solitary bees can be affected by stressors, such as pesticides, differently from honey bees (Brittain and Potts 2011, Uhl and Brühl 2019). This fact was noted by EFSA, which suggested including *O. bicornis* as a model organism for non-*Apis* solitary bees in the pesticide risk assessment scheme (EFSA 2013). Therefore, an individual-based model of *O. bicornis* will supplement the honey bee colony model to understand better the impact of various stressors on pollinators and the services they provide.

Aim and purpose

The ALMaSS model of *O. bicornis* aims to provide a realistic and detailed representation of *O. bicornis* populations in space and time in European agricultural landscapes. The model should be able to generate emergent population patterns, based on landscape and management context. The model will be used to:

•   Evaluate the impact of agricultural management and pesticide use on these bees;
•   Explore factors that could lead to pollinator decline in agricultural landscapes;
•   Be a candidate model for use in pesticide regulatory risk assessment in a systems-based approach;
•   Provide a framework in which to assess the current state of *Osmia* knowledge;
•   Provide a starting point for the development of future solitary bee models.

Theoretical framework and modelling approach

Here, we use an agent-based modelling approach (Grimm and Railsback 2005). Each bee is represented as a separate object of a particular state with given properties, such as age or size. Characteristics such as bee age and size are important, as they influence many bee traits (Everaars and Dormann 2014). These are related to foraging, dispersal, reproduction and provisioning, thus affecting total reproductive potential, the sex ratio of progeny in a nest, progeny cocoon *mass* or the required amount of pollen for a single brood cell. We assume that *O. bicornis* females balance offspring size and number following the optimal allocation theory (Smith and Fretwell 1974). However, local environmental factors will modify the actual parental investment decision (i.e. the amount of provision provided to a brood cell) (Seidelmann 2018).

Our model is spatially explicit; the position of a bee and its nest are both simulated. The ALMaSS modelling environment also provides a detailed spatio-temporal representation of the landscape from which individual bees obtain the information necessary to simulate their behaviour. This representation describes spatial landscape heterogeneity through a detailed raster land-cover map with a spatial resolution of 1 m^2. Farmed areas are represented as accurate maps of fields grouped into farm units of different types (e.g. cattle or arable farms). The temporal component of agricultural landscape heterogeneity refers to crop management throughout a year, described through individually-tailored management plans for each crop. The cropping system is understood as a pluri-annual crop rotation. Crop management plans consist of combinations of farm activities (including pesticide treatments), time windows and probabilities of carrying out these activities. The temporal component includes weather conditions and vegetation growth models for all modelled vegetation types and crops; this is all updated daily. Such an approach gives a highly realistic dynamic landscape simulation with vegetation growing in response to the weather and the pattern of farming activities related to each specific crop, farm and field (Topping et al. 2016). The resource-providing units are the vital elements of the landscape simulation for bees. These define the quantity and quality of pollen and nectar for each habitat patch and the density of nesting sites (described in section "Use for resources").

The model will consider the behaviour of all bee life stages daily. The model's parameters are based on field and laboratory data on *O. bicornis* available in literature and from our own experiments (performed by the Terrestrial Ecosystems and Ecotoxicology Group, Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland). When the necessary data were not available for *O. bicornis*, we estimated parameters, based on published data from other species of the *Osmia* genus with similar life history, particularly *O. cornuta* (European orchard bee, slightly larger than *O. bicornis*), *O. cornifrons* (Asian sister species) and *O. lignaria* (North American sister species).

Framing the model

The red mason bee *O. bicornis* is an important pollinator in agricultural landscapes. It is often reared on a commercial scale to be used as a managed alternative pollinator, especially in orchards (Biliński and Teper 2004, Teper and Biliński 2009, Gruber et al. 2011). It is commonly used for laboratory and field studies on wild bees, including studies of pesticide toxicity, effects of environmental pollution or ecological stoichiometry (Szentgyörgyi et al. 2017, Filipiak 2019, Mokkapati et al. 2021) and, thus, its biology and ecology are relatively well known. Data on other species in the *Osmia* genus with similar life histories are also available (Bosch et al. 2008), supporting findings for the *O. bicornis*. *Osmia* spp. are known to be polylectic/polylege, which means that they are pollen generalists collecting food resources from the flowers of various plants depending on their availability (Raw 1974, Haider et al. 2014, Kratschmer et al. 2020, Bednarska et al. 2022). Hence, the *Osmia* model will be for the more robust solitary bees, which needs consideration if the model aims to represent a wider group of species later.

Some limitations must also be considered related to the nature of the available data. Laboratory studies investigating the developmental time of *O. bicornis* in various temperature regimes were carried out on populations reared in Poland and Germany and, thus, may not represent populations from other climatic regions. Similarly, following Kemp and Bosch (2005) and Bosch et al. (2008), we assume that the duration of prepupal diapause is the main mechanism through which populations of *Osmia* spp. synchronise adult eclosion with local temperature declines in the autumn. Furthermore, the temperature experienced by *Osmia* spp. bees during pre-wintering and winter diapause affects mortality during overwintering and the spring's emergence timing (Bosch et al. 2010, Sgolastra et al. 2011). All these assumptions mean that caution is needed when using the model for regions with different climatic conditions.

Populations of wild bees depend on the spatial distribution of nesting and foraging habitats and it has been suggested that *O. bicornis* is strongly constrained by nesting site availability (e.g. Steffan-Dewenter and Schiele 2008). However, there is a lack of field studies on populations in their natural environment that would allow characterisation of the natural breeding locations and population sizes. *O. bicornis* is quite flexible in selecting cavities for nesting (using plant stems, dead wood, wooden fences or holes between brick walls) (Raw 1972); thus, estimating the possible nesting density for a given habitat type becomes difficult. Classifying land-cover/land-use elements qualitatively into those

providing poor and abundant nesting resources (Everaars et al. 2011) does not provide enough information for an individual-based model. Therefore, we suggest estimating nesting density in different habitat types, based on the cavity nesting suitability provided by Koh et al. (2016). The categories of land-cover/land-use elements used by Koh et al. (2016) are quite broad and the study does not consider any microsite attributes (e.g. sun exposure) which may play an important role. Hence, if these densities are not representative of typical nesting densities, this will alter the model's outcome.

According to many studies, food is not a limiting factor for *O. bicornis* in the field (Everaars et al. 2011, Coudrain et al. 2016). However, these studies focused on evaluating food provided for larvae. It is unclear how the availability of adult food (mainly nectar) and competition with other pollinators can influence that assumption. The impact of the interplay between the spatial and temporal distribution of food resources (both for larvae and adults), nesting resources and additional resources, such as nest-building material on long-term population dynamics, has not yet been fully investigated. Furthermore, the number of offspring produced can be strongly affected by parasitoids, whose abundance also varies in space and time.

In the first version of the *O. bicornis* model, we will assume that adult bees are not limited by food availability for themselves and that the nest-building material is unlimited. The impact of pollen quantity on maternal investment will be considered. However, we will not account for either *O. bicornis* preference towards certain types of pollen or the influence of pollen quality on the offspring. We will not model energy intake and consumption by individual bees during foraging and dispersal. Nevertheless, the pollen search algorithm will include the distance from the nest to favour closely-available pollen resources (see section "Use of resources"). Competition from other pollinators will be modelled as a decrease in the floral resources available to *O. bicornis* (controlled by the *OsmiaDensityDependentPollenRemovalConst* parameter). The assessment of parasitoids will be simplified by not explicitly modelling parasitoid populations. Instead, the risk of open-cell parasitism will increase with the time the cell is open (Seidelmann 2006). The time step in the model will be one day, also for the assessment of resources. These limitations and their possible impacts on the model are revisited in the "Discussion" section.

Although the model is aimed towards use for pesticide risk assessment, the first version of the model will only consider that pesticides are present in the environment and we will not include specific pesticide handling processes. This is because we assume that these will be specific to any particular pesticide scenario and that exposure procedures developed for ApisRAM (Duan et al. 2022) will be used for *O. bicornis* model in its next version.

Overview of processes

The red mason bee is a univoltine (one generation per year), polylactic/polylege solitary species of the *Osmia* genus, common in central and northern Europe (Raw 1972). Its flying season starts in spring and continues until early summer (Steffan-Dewenter and Schiele

2008). Males appear approximately a week earlier than females (protoandry) and have a shorter life span compared to females (Raw 1972). According to our laboratory data, the male adults developed in natural conditions may live up to 38 days, while adult females up to 90 days. *Osmia* populations from warmer geographical areas start their flying season earlier. For example, Felicioli et al. (2018) reported that, in Italy, *O. bicornis* is active from February to April, while in Poland, the first individuals appear much later, in March/April and fly until June (Szentgyörgyi and Woyciechowski 2013). Similar differences in bee phenology were found between geographically-distinct populations for *O. cornuta* and *O. lignaria*. According to Sgolastra et al. (2011), even populations from areas separated by less than 200 km, but with distinctly different mean annual temperatures, differ in the timing of the flying period. For example, *O. cornuta* from Tarragona, Spain (mean annual temperature of 15.6°C), flies from February through to the middle of March, while *O. cornuta* from Girona, Spain (mean annual temperature of 12.4°C), flies from the middle of March through to April.

O. bicornis females are monandrous and males are polygamous (Szentgyörgyi and Woyciechowski 2013, Giejdasz and Fliszkiewicz 2016). They accept diverse pre-existing cavities as nest sites, usually tube-shaped. After finding a suitable nesting place, bees enter the reproduction phase. Within their lifetime, females construct sequentially several nests of the line type; cell after cell in linear order separated by mud partitions. Each brood cell is dedicated to one egg, which the mother bee provisions with pollen with a low proportion of nectar (Maddocks and Paulus 1987, Strohm et al. 2002). Usually, female progeny is laid deeper inside the nest (inner brood cells) and male progeny toward the nest entrance (outer brood cells) (Ivanov 2006, Szentgyörgyi and Woyciechowski 2013), although exceptions occur more or less frequently (Strohm et al. 2002; authors' field data).

The development of the red mason bee is similar to that of other spring species of the *Osmia* genus. It can be categorised into six main life stages: egg, larva, prepupa, pupa, cocooned adult and adult. Life stages from egg to cocooned adult occur inside the nest. Egg laying and larval development occur in spring, while prepupal and pupal stages occur in summer. The imago instar appears in the cocoon at the end of summer/beginning of autumn. The cocooned adult is the overwintering form of the red mason bee (Raw 1972, Sedivy and Dorn 2014) (Fig. 1). Only adults, after emerging from the cocoon, interact with the local landscape/environment as the females, after being fertilised by males (whose role is limited to insemination; Raw (1972)), move within the landscape to look for nesting places and food resources to be able to provision offspring with pollen.

Life stages

Each year, a new generation of bees appears in spring. After finding a suitable nesting place, bees enter the reproduction phase. A mother bee builds a separate brood cell for each egg, which she provisions with pollen and a low proportion of nectar. The further development can be summarised as follows (the details of development and overwintering

drivers with references are described in sections "Development in the nest" and "Overwintering", respectively):

- The mother bee places an egg on top of the provision. The egg could be fertilised (female-diploid progeny) or non-fertilised (male-haploid progeny). The duration of the egg stage is sex-independent, but temperature-dependent, so it is shorter at higher temperatures. The egg develops into a larva;
- After hatching from the egg, the larva eats from the provision available in the cell (and defecates) until the start of cocoon formation (spinning larva). Apart from eating, the movements of larvae are limited. Except for the spinning substage, the larval stage duration is sex-dependent, shorter for males than females and temperature-dependent, shorter at higher temperatures. The larva develops into a prepupa;
- The cocooned larva enters prepupal dormancy more or less in synchrony with early summer. The duration of the prepupal stage is sex-dependent, shorter for males than females and temperature-dependent (but non-linearly). The prepupal stage lasts around 1-3 months, depending on the geographical area. During this stage, the respiration rate drops significantly and body weight loss is minimal. Temperatures above a certain threshold are required for the completion of prepupal dormancy. The prepupa develops into a pupa;
- The duration of the pupa stage is sex-dependent, shorter for males than females and temperature-dependent, shorter at higher temperatures. The pupa develops into a cocooned adult in late summer/early autumn;
- The adult overwinters in the cocoon and emerges from the nest the following spring. The overwintering period can be divided into prewintering, diapause and post-diapause. The initiation of the prewintering does not require a temperature or photoperiod signal; rather, it is a fixed component of the ontogenic bee programme. However, the transition to winter diapause is triggered by low wintering temperatures.

Planned implementation in the model

The model will include all six-life stages of *O. bicornis* female individuals. It is assumed that all adult females are being fertilised, therefore, we will not model mating activity. The males will not be included in the model, except for the nesting and provisioning activities of the mother (further information is provided in sections "Nesting" and "Provisioning"). The development within the nest (from egg to cocooned adult) will be modelled according to the in-nest life-stage state machine and transition path (Fig. 2). After emergence from the nest in spring, adult fertilised female bees will start to interact with the environment, i.e. to disperse to look for nesting and food resources, provision the nests with pollen and reproduce (see further sections for more details). Although provisions contain a small amount of nectar, for the purposes of our model, we assume that nectar is not a limiting factor, hence only pollen resources and the search for pollen will be considered.
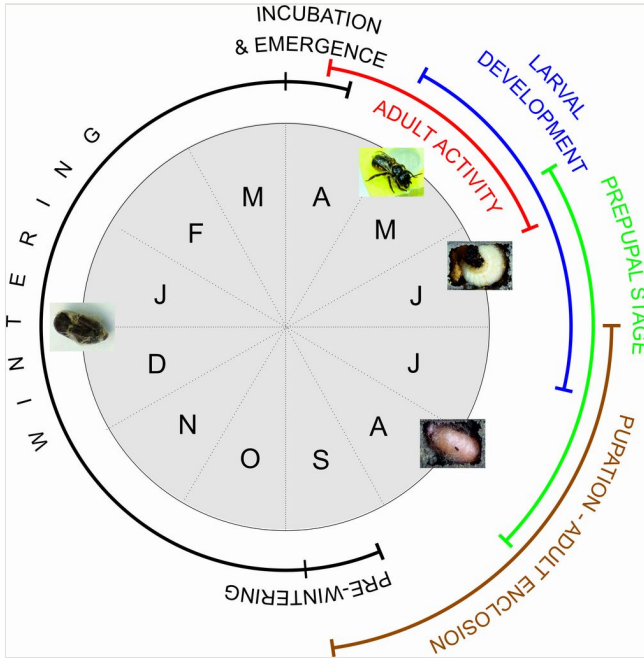
Figure 1. doi

Typical red mason bee (*O. bicornis*) developmental cycle for central European populations (based on Giejdasz and Wilkaniec (2002), Radmacher and Strohm (2011)).
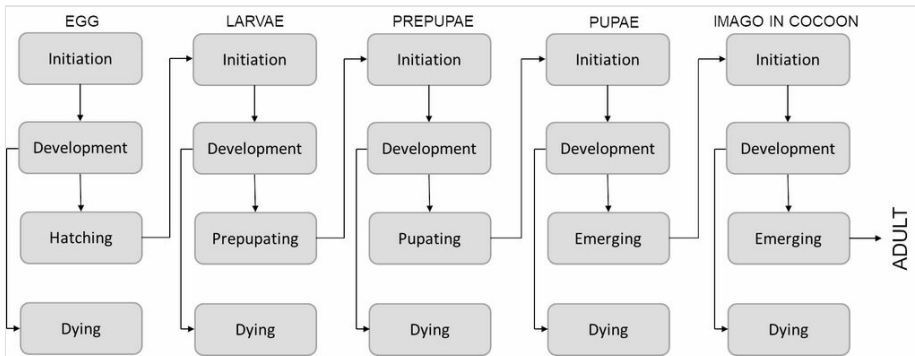

Figure 2. doi

Red mason bee (*O. bicornis*) state diagram showing development within the nest.

Bees of all life stages will have some common attributes, such as the duration of the life stage measured in both days and accumulated degree days (Table 1). The *mass* of an adult bee will be a derivative of the *mass* of provisions collected by a mother bee and the changes in *mass* between life stages will not be tracked (see section "*Osmia mass*"). Each day, besides the overwintering period (i.e. during cocooned adult life stage), the bee experiences a daily probability of mortality (Table 1).

Table 1.

State variables with units common for all life stages of *O. bicornis*. These will be explained in greater detail in the text that follows.

Variable name	Units	Description
Stage age	days	How many days in this life stage
Sex	female/male	Allocation of sex. For eggs: female = fertilised, male = unfertilised. After the egg stage, the unfertilised eggs will not be tracked in the model
Mass	mg	The *mass* of provision gathered in the brood cell for a larva or *mass* of an adult bee being a derivative of the provision *mass*
Accumulated degree days	degree days	How many degree days are accumulated
Target degree days	degree days	How many degree days are needed to transition to the next stage or trigger some type of behaviour
Daily mortality	daily probability of death	The mortality experienced in a given life stage besides overwintering

Development in the nest

The early and late flying populations of the same *Osmia* species have different durations of the developmental cycle. For example, Sgolastra et al. (2012) reported that, in natural conditions, the duration of the developmental cycle of early-flying (March), *O. lignaria* takes around 170 days, while for the late-flying population (May) of the same species, it is around 110 days. The longer developmental time of early flying populations was also found when populations were tested under laboratory conditions (i.e. with the same stable or fluctuating temperatures; Sgolastra et al. (2012)). Therefore, analysing or merging data on developmental rates from geographically-distinct locations should be done with caution.

Duration of in-nest development is temperature driven, such that higher temperatures lead to faster development of eggs, larvae and pupa (Table 2). The relationship between the duration of the prepupal stage and temperature is non-linear. The highest prepupal developmental rates are attained at intermediate temperatures (Bosch et al. 2008). That was reported for *O. cornuta* by Sgolastra et al. (2012), but is also supported by the data for *O. bicornis* from Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016) (Table 2, Fig. 3). According to Kemp and Bosch (2005) and Bosch et al. (2008), the duration of the prepupal diapause is the main mechanism through which populations of *Osmia* spp. from different geographical areas synchronise adult eclosion with local temperature declines in the autumn.

Planned implementation in the model

In the model, the transition to the next developmental stage for the eggs, larvae and pupae (Fig. 2) will occur when the sum of effective temperatures (SET) or, in other words, the accumulated degree days attributed reaches a certain threshold (Table 3). Different lower developmental thresholds (LDTs), also known as basal temperatures (T_b), will be used for

each of the life stages to calculate SET. The LDTs are calculated in such a way to provide the minimum covariance for the data from Table 2.

Table 2.

Summary of studies investigating temperature-driven development of *O. bicornis* in the nest. Only data on females are shown.

Reference	Temperature (°C)	Duration (days)					
		Egg	Larva	Prepupa	Pupa	Prepupa + pupa	Total development
Natural conditions							
Giejdasz and Wilkaniec (2002)	-	7.6	39.1	-	-	54.2	100.9
Radmacher and Strohm (2011)	-	7	34	25	36	61	102
Laboratory conditions							
Radmacher and Strohm (2011)	17.5	8	32	32	54	86	126
Giejdasz and Fliszkiewicz (2016)	20	3	36	28	32	60	99
Radmacher and Strohm (2011)	22.5	5	32	25	30	55	92
Giejdasz and Fliszkiewicz (2016)	25	3.2	28	24	29	53	84.2
Radmacher and Strohm (2011)	27.5	4	20	42	20	62	86
Giejdasz and Wilkaniec (2002)	28	3.1	19.7	36.3	10.9	47.2	70
Giejdasz and Fliszkiewicz (2016)	30	2	27	31.2	23.1	54.3	83.3

Table 3.

Parameters for temperature-driven development of *O. bicornis* in the nest (based on data from Table 2).

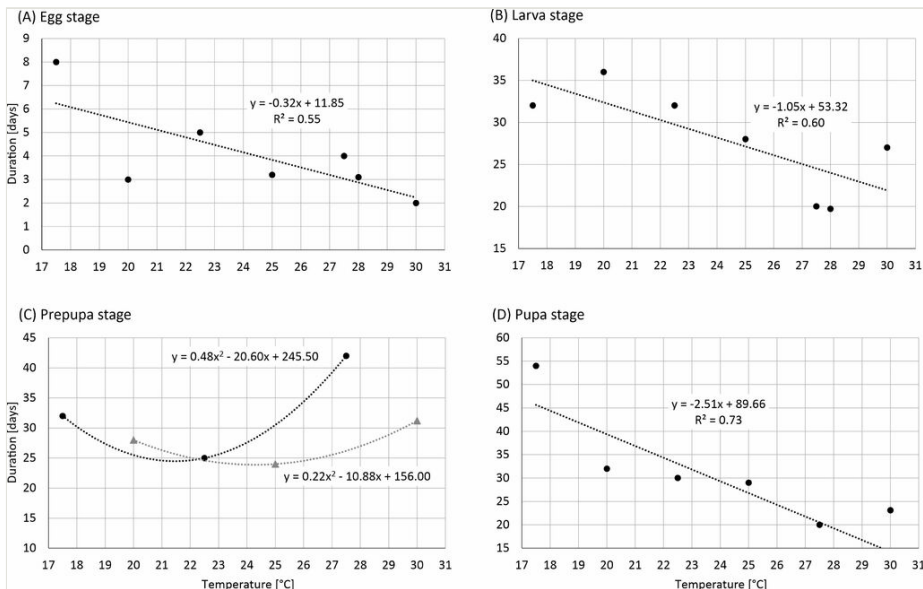| *Osmia* life stage	Lower developmental threshold (LDT) in °C	Sum of effective temperatures (SET) in degree days
Egg	13.8	37.0
Larva	8.5	422.4
Pupa	13.2	272.3

Figure 3. [doi]

Relationship between duration of *O. bicornis* female developmental stages and temperature. For egg, larva and pupa, we combined the results obtained by Giejdasz and Wilkaniec (2002), Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016); for prepupa, results from Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016) were analysed separately.

The duration of the prepupal stage will be related to the temperature using a quadratic function (a mean of the functions presented in Fig. 3C) with an optimum at 22°C, at which the maximal developmental speed of 24.3 days is reached. In addition, an individual variation will be built in around a maximal developmental speed (+/- 10%).

During each developmental stage there is a probability of dying (see section "Mortality"), generally dependent on the temperature profiles. *O. bicornis* will also be affected by open-nest parasitism (see section "Parasitism").

Overwintering

The overwintering period of *O. bicornis* can be divided into three parts: pre-wintering, diapause (wintering) and post-diapause quiescence. In central Europe, pre-wintering occurs in September – November, diapause in November – January and post-diapause quiescence in February – March. The photoperiod has not been implicated in overwintering, since development from the egg to the adult in this species takes place inside a sealed nest in complete darkness. The initiation of pre-wintering does not require a temperature signal either; rather, it is a fixed component of the ontogenic bee programme (Bosch et al. 2010).

Although no studies on triggers for diapause have been conducted on *O. bicornis*, important results can be found for *O. lignaria* and *O. cornuta*. It was shown that respiration rates for overwintered bees under both natural and experimental conditions follow the same pattern. There is an abrupt drop in respiration shortly after adult eclosion, then a sharp increase in coincidence with a strong decline in ambient temperatures, followed by a further slow, steady increase throughout the winter (Bosch et al. 2010). Therefore, from a physiological perspective, pre-wintering in *Osmia* species may be defined as the period between adult eclosion and the increase in respiration rate prompted by the onset of winter temperatures (Bosch et al. 2008, Bosch et al. 2010). For *O. lignaria* from northern Utah, USA, Sgolastra et al. (2011) proposed using temperatures below 15°C as the trigger of the diapause stage.

A proper definition of the transition between pre-wintering and diapause is important, as the duration of pre-wintering has important consequences for the diapause development, winter survival and the bee's vigour at emergence in spring. Increased duration of pre-wintering leads to an increase in body-fat depletion and decreases the post-emergence longevity without feeding (Bosch et al. 2010).

During diapause, the value of the supercooling point (i.e. the temperature threshold above which the body of the bee does not freeze) decreases. Diapause lasts about 100 days and seems to be independent of temperature variation. After this period, in post-diapause, bees develop normally, but their development is inhibited by the temperature (higher temperatures shorten the duration of post-diapause). At the beginning of post-diapause, their supercooling point increases gradually until spring.

Planned implementation in the model

In the model, the pre-wintering period will be defined as the period from adult eclosion (end of the pupa stage) to the time threshold *D*, determined, based on the temperature regime as defined below.

For every day *d* after 1 September, we will be checking the average daily temperature T_{avg}, in order to detect a sharp and stable temperature drop:

If

$(T_{avg}(d-5) - T_{avg}(d-4) \geq 1°C)$ and $(T_{avg}(d-4) - T_{avg}(d-3) \geq 1°C)$

and $T_{avg}(d-2)$ and $T_{avg}(d-1)$ and $T_{avg}(d) < 13°C$ (Eq. 1)

Or

$(T_{avg}(d-5) - T_{avg}(d-4) \geq 3°C)$ and $T_{avg}(d-3)$ and $T_{avg}(d-2)$ and

$T_{avg}(d-1)$ and $T_{avg}(d) < 13°C$ (Eq. 2)

$Then threshold D = d$

In Sgolastra et al. (2011), the time threshold *D* was defined as the last day with a temperature higher than 15°C. However, the direct implementation of this rule in the model would mean that the bee can predict future temperatures. In contrast, we propose to apply rules, based on temperatures currently experienced by bees (so no predictions are required) and allow the capture of sudden temperature drops below 15°C, followed by 5 days with low enough temperatures. The onset of winter will then be defined at the end of this cold period. Such a solution seems to predict the onset of winter well in Polish conditions and, at the same time, shows results similar to those presented by Sgolastra et al. (2011) (Fig. 4).
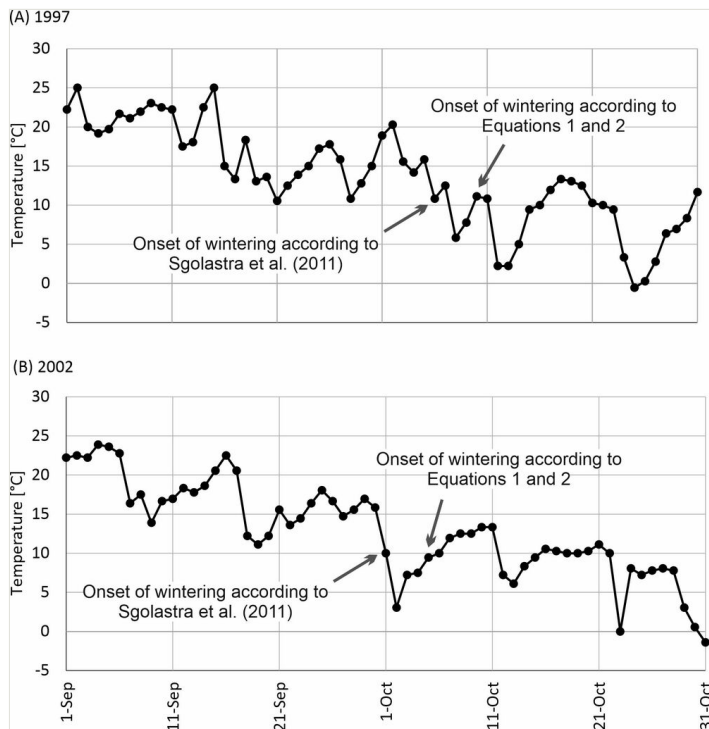

Figure 4. doi

Application of rules to predict the onset of wintering according to this work (Equations 1 and 2) and Sgolastra et al. (2011) for two exemplary years, 1997 (A) and 2002 (B), in North Logan, Utah, USA. Years presented here correspond with the ones in Sgolastra et al. (2011).

In our model, the temperature conditions during pre-wintering will influence the bee's overwintering mortality (see section "Mortality"), while temperature conditions during diapause – the timing of bee's emergence from the nest on spring (see section "Emergence from the nest"). The impact of the duration of the pre-wintering on the longevity of bees will not be considered as there is evidence that prolonged pre-wintering duration does not affect post-emergence longevity in nature, probably because emerging females could rapidly replenish their metabolic reserves through feeding (Sgolastra et al. 2016).

Emergence from the nest

The start of emergence from the nest for bees of the *Osmia* genus depends on the overwintering temperatures (Bosch and Kemp 2004, Fründ et al. 2013), such that the warmer the winter is, the earlier bees start to emerge. Fründ et al. (2013) found a linear relationship between wintering temperatures (stable wintering temperatures under laboratory conditions) and the start of emergence, measured as the number of days from the beginning of incubation on 1 March, when bees were brought to an incubation room with temperatures of 12-17°C, simulating a spring increase in outdoor temperatures. According to personal communication with J. Fründ, this relationship is given by an equation:

$$noDaysToEmerge = 39.4819 - 1.70001 \times mean\_temp \text{ (Eq. 3)}$$

Not all bees emerge from the nest/nests on the same day. The curves of the cumulative percentage of emerged females are sigmoid-shaped (Giejdasz and Wasielewski 2017; Fig. 5). In addition, emergence dynamics changed depending on the incubation time, i.e. when the bees were transferred to warmer temperatures. Giejdasz and Wasielewski (2017) showed that an artificially extended wintering period results in shorter times to emergence and earlier occurring 'peak' of emergence rates (Fig. 5).
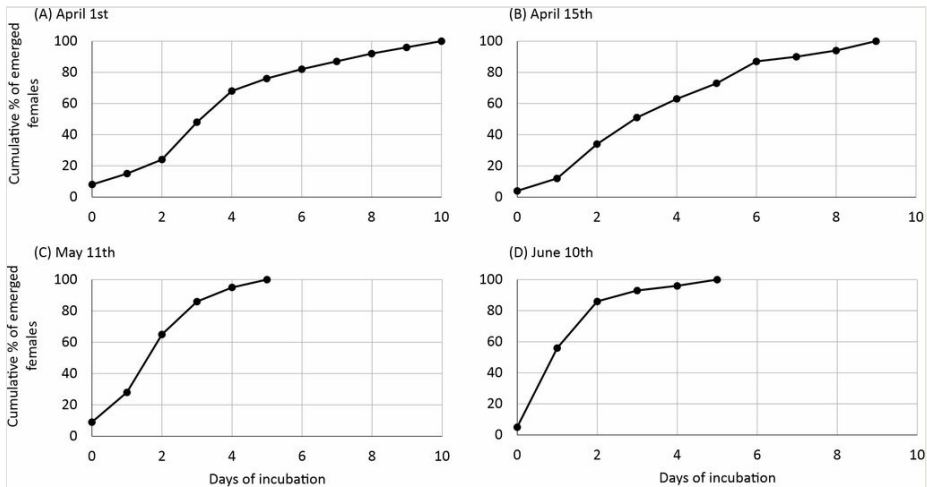

Figure 5. doi
Cumulative percentage of emerged *O. bicornis* females as a function of the number of days since the beginning of incubation, at various terms (based on data from Giejdasz and Wasielewski (2017)).

Planned implementation in the model

In the model, we will relate the beginning of emergence to the accumulated degree days during the wintering period, according to Fründ et al. (2013):

$$noDaysToEmerge = 39.48 - 0.0147 \times \sum(DD\_winter)$$ (Eq. 4)

where *noDaysToEmerge* is the number of days to the beginning of emergence after 1 March with a mean daily temperature above a certain threshold and *Σ(DD_winter)* is the number of accumulated degree days with baseline temperature $T_0 = 0°C$, during the wintering period as defined in section "Overwintering".

The emergence distribution was implemented according to data provided by A. Bednarska (personal communication; data come from the lab experiment where bees were overwintered at 4 degrees and, on 11 April, were moved to 20 degrees; Fig. 6). We decided not to use the results of Giejdasz and Wasielewski (2017), as they incubated bees at a very high temperature of 28°C, which rarely occurs in spring under natural conditions for a longer time. Furthermore, under natural conditions, bees rarely emerge after the second half of April. Therefore, extremely shortened emergence distributions shown in Fig. 5C and D are not likely to occur and emergence patterns for earlier terms (1 April and 15 April , Fig. 5A and B) are similar to those arising from the data provided by A. Bednarska.
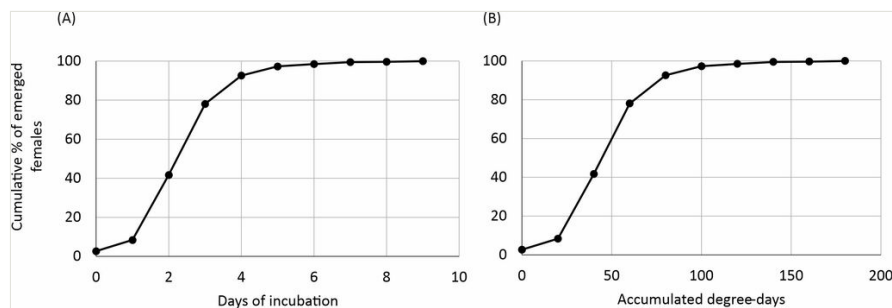

Figure 6. doi

Cumulative percentage of emerged *O. bicornis* females on consecutive days of cocoon incubation after their transferring from overwintering in 4°C to 20°C (based on data from laboratory experiment provided by A. Bednarska).

Osmia mass

In solitary bees, progeny body size is largely determined by maternal provisions and microclimate (Radmacher and Strohm 2010).

Cocooned adult *mass*

Cocooned adult *mass* increases with provision *mass* (Ivanov 2006, Seidelmann 2006, Radmacher and Strohm 2010) and decreases with increasing temperature during larval development (Radmacher and Strohm 2010). According to the laboratory experiment by Radmacher and Strohm (2010), higher temperatures during larval development lead to higher mortality (of larvae) and smaller body *mass*, partly due to incomplete consumption of the provisions, i.e. at higher temperatures, there are more pollen remnants (Table 4). However, under natural conditions (i.e. fluctuating temperatures), pollen remnants occur

rarely in *O. bicornis* nests (Ivanov 2006, Seidelmann 2006; personal investigations). In this case, the *mass* of cocooned adults can be defined as being proportional to the *mass* of provisions.


Table 4.

Relationship between pollen provisions and cocooned adult *mass* of *O. bicornis* (based on data from Radmacher and Strohm (2010)).

Temperature	Duration of larva to cocooned adult stages (according to Giejdasz and Fliszkiewicz (2016))		Relationship between cocooned adult *mass* [mg] (y) and *mass* of consumed pollen (x) for females [mg]	Mean *mass* of pollen remnants [mg]
	Days	**Accumulated degree days**		
20	96	1920	y = 0.23*x +57	0
25	81	2025	y = 0.34*x-1	3.85
30	81.3	2439	y = 0.29*x-6	119.23

Adult bee *mass*

The fresh *mass* of adult females after emergence can vary considerably from 25 to 150 mg (Fig. 7) and depends on the *mass* of cocooned adults and, therefore, the amount of provision in the brood cell. It may also depend on overwintering temperatures as the *mass* loss during winter is slightly higher in warmer conditions (Fründ et al. 2013). The adult bee *mass* decreases during the flight season, mainly due to the high energy expenditure for reproduction. The rate of this loss depends on the bee's initial *mass*, i.e. is significantly more pronounced in smaller females (Strohm et al. 2002).
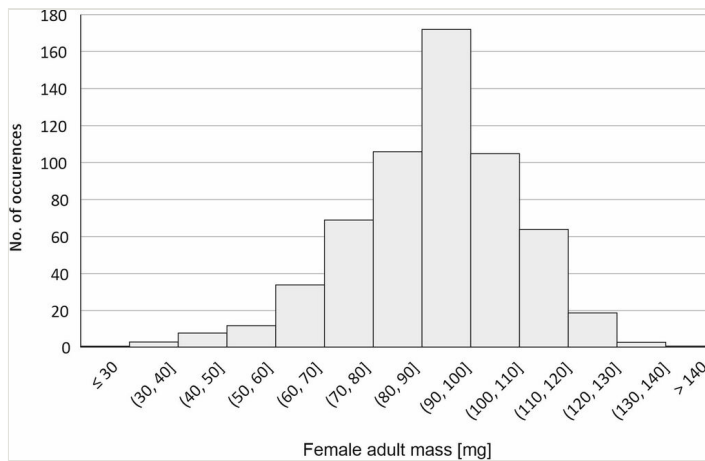
Figure 7. doi

Distribution of *O. bicornis* female fresh *mass* after emergence (n = 597). Based on data provided by A. Bednarska.

Planned implementation in the model

We will assume that the larva consumes all provided pollen. This is because, under natural conditions, the larva does not experience extreme temperatures > 30°C for a long enough time to cause substantial pollen remnants as reported by Radmacher and Strohm (2010).

The following formulae will be implemented to calculate the *mass* of cocooned adults from the provision *mass* derived, based on Seidelmann (2006):

$$femaleCocoonedMass = \frac{provisionMass}{3.247}$$
(Eq. 5)

$$maleCocoonedMass = \frac{provisionMass}{3.597}$$
(Eq. 6)

where *provisionMass* is the *mass* of pollen available in the nesting cell and all masses are in [mg].

It is noted that the *mass* of the cocooned male is not used directly as a life stage attribute (as males are not tracked in the modelling past the egg stage), but Equations 5 and 6 are both used by the mother bee in the provisioning plan (see section "Provisioning").

Since, according to Fründ et al. (2013), the mean loss of *mass* during overwintering can differ only by up to ~ 3% depending on overwintering temperatures, in the model, we will assume that the loss of *mass* during overwintering is temperature independent and, therefore, a linear relationship between the *mass* of the cocooned female and the *mass* of the female adult can be accepted. We will use the equation provided by Seidelmann et al. (2010):

$$femaleAdultMass = 0.80 \times femaleCocoonedMass + 4.00$$
(Eq. 7)

In the code, each bee after emergence from the nest will obtain a *mass* property as a direct function of the *mass* of provision available in the nest cell from which the bee originates. This function will be a combination of two linear relationships, one predicting the *mass* of the cocooned adult from the *mass* of provision (Equation 5) and the second predicting the *mass* of the adult bee from the *mass* of cocooned adult (Equation 7):

$$femaleAdultMass = 0.25 \times provisionMass + 4.00$$
(Eq. 8)

We are aware that body *mass* decreases during the flight season. However, this will not be tracked during the simulation. Instead, the model will use a provisioning efficiency variable related to the age of the bee (see section "Provisioning").

In the model, two classifications of adult female bees, based on their *mass*, will be used:

- *BeeSizeScore1* - will use four size classes: very small (0), small (1), medium (2) and large (3) calculated according to Equation 9. BeeSizeScore1 will be used to calculate the number of eggs in the first nest built by a bee (see section "Nesting");

$$BeeSizeScore1 = int(floor(\frac{adultFemaleMass - OsmiaFemaleMassMin}{(OsmiaFemaleMassmax - OsmiaFemaleMassMin)/3.0} + 0.5))$$

(Eq. 9)

- *BeeSizeScore2* – will use smaller classes of bee sizes with size class controlled by the *OsmiaAdultMassCategoryStep* variable and is calculated according to Equation 10. BeeSizeScore2 will be used in the calculation of foraging and dispersal distances (see section "Foraging and dispersal"), the planned sex ratio of female vs. male progeny in a given nest (see section "Reproduction) and the planned *mass* of provision needed for each egg (see section "Provisioning").

$$BeeSizeScore2 = int(floor(\frac{adultFemaleMass - OsmiaFemaleMassMin}{OsmiaAdultMassCategoryStep} + 0.5))$$

(Eq. 10)

Foraging and dispersal

We can differentiate between the bee's homing distance and foraging distance. Homing distance is the maximum distance from which a bee can find its nest. Homing distance differs for individuals of the same species, indicating that some bees have been further from the nest in their life than other bees (Gathmann and Tscharntke 2002). Despite differences between individuals, the distance at which 50% (as well as 10%) of the individuals are able to return can be considered as a species trait and relates to body size measured through intertegular (IT) span (based on data collected in earlier homing studies of 16 bee species; Greenleaf et al. (2007)):

$$\log_{10}(r90) = -1.363 + 3.366 \times \log_{10}(IT\_span)$$ (Eq. 11)

$$\log_{10}(r50) = -1.643 + 3.242 \times \log_{10}(IT\_span)$$ (Eq. 12)

where *r90* is the maximum homing distance (i.e. the distance at which 10% of bees are able to return to the nest) in [km], *r50* is the typical homing distance (i.e. the distance at which 50% of bees are able to return to the nest) in [km] and *IT_span* is the intertegular span in [mm].

The foraging range includes inbound and outbound flights from the nest to the resources and varies with the spatial and temporal availability of resources in the landscape (Guédot et al. 2009). The maximum foraging range is sometimes confusingly equalled with the maximum homing distance (normally the maximum foraging distance < maximum homing distance). The maximum homing distance is given by an individual that has flown very far and has a wide knowledge of the environment. It may even be that this individual has come

from far away looking for a nest. The maximum homing distance is, thus, far beyond the everyday foraging activity of a species.

According to the general Equations 11 and 12, *O. bicornis* female weighing 92.63 mg (mean body *mass* according to the data provided by A. Bednarska; see Fig. 7; sd = 17.36) has *r50* of 0.97 km and *r90* of 2.13 km. These values are much higher than those provided by Gathmann and Tscharntke (2002), where *r50* for *O. bicornis* was estimated as ~ 0.5 km and *r90* as ~0.95 km. However, pollen analysis conducted for *O. bicornis* in the Wielkopolska region (Poland) showed that bees collected oak pollen for their offspring even if oak trees were located ~ 1 km from the nest.

Implementation in the model

In the model, two different types of movement will be considered: long-range (dispersal) and short-range. The long-range movement will be used when looking for a new nesting site if there are no nesting sites available in the surroundings of the previous nest or the resources available around the nest are too low to allow for nesting. In the model, the dispersal distance will be related to the maximum homing distance *r90*, i.e. *r90* will be used as a rescaling parameter to the general movement distribution defined as the beta distribution *X ~ Beta(α, β)* with assumed parameters *α* = 10 and *β* = 5 (Figure 8). *r90* will be calculated according to Equation 11 and, therefore, will be related to the bee *mass* through the intertegular span, *IT_span*. The intertegular span will not be directly introduced in the model, but we will calculate it from the body *mass* of the bee, based on the equations provided by Greenleaf et al. (2007):

$IT\_span = 0.77 \times dryBodyMass^{0.405}$ (Eq. 13)

$dryBodyMass = 1.219 \times 10^{-4} + 0.358 \times femaleAdultMass$ (Eq. 14)

The short-range movement will be used to evaluate food resources around the nest (i.e. food resource availability will be assessed in the vicinity of the nest defined by the bee's foraging distance; see section "Use of resources"). As no studies show foraging histograms for *O. bicornis* (no capture-mark-recapture studies with enough observations), in the model, the foraging distance will be related to the typical homing distance *r50*, that is, *r50* will be used as a rescaling parameter to the general movement distribution defined as the beta distribution *X ~ Beta(α, β)* with assumed parameters α = 10 and β = 5 (Fig. 8). *r50* will be calculated according to Equation 12.

We decided to use Equations 11 and 12 to calculate *r90* and *r50*, even if they are based on data from homing studies for 16 different bee species rather than for *O. bicornis*, as these are the only available data that allow relating movement to bee size. Although Gathmann and Tscharntke (2002) reported *r50* and *r90* values for *O. bicornis*, they were not related to the body size of the bee, but were provided as parameters for the entire population (with unknown characteristics).
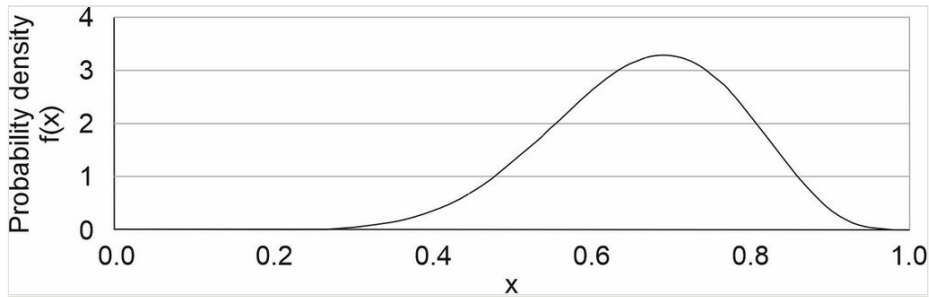
Figure 8. doi

The general movement distribution of *O. bicornis* females is defined as beta distribution $X \sim Beta\ (\alpha,\ \beta)$ with parameters $\alpha = 10$ and $\beta = 5$.

Nesting

Pre-nesting

Immediately after mating, females are rarely seen around their natal nesting site and they use this time for feeding and to complete ovary maturation. The pre-nesting period is usually 2-5 days, but it may be longer due to bad weather conditions (Bosch et al. 2008).

Searching for a nest

After the pre-nesting period, bees return to their natal nesting site to check for empty nesting places in the surroundings (within a distance defined by the typical homing distance $r50$, see section "Foraging and dispersal"). If free nesting sites are unavailable in the vicinity closest to the natal nesting site, then dispersal occurs to look for new nesting sites outside the foraging distance (within maximum homing distance range $r90$). If there are still some eggs left to lay after constructing a first nest, the bee will look again for a new nesting site.

Structure of a nest

When building their nests, females of *O. bicornis* use pre-existing cavities, which are usually tube-shaped. The bees are readily attracted to holes in dry stems of hollow plants (e.g. the common reed), dead wood or even cavities in building walls or wooden fences. The cells in the nest are arranged linearly in series with transverse partitions between, built by the female who collects mud and mixes it with saliva. According to Ivanov (2006) and Seidelmann et al. (2016), female bees can accept a wide spectrum of nest dimensions, both in terms of length (5-30 cm) and diameter (4-12 mm). Depending on the length of available nesting material (the longer the cavity/reed, the more cells are built), the bee can build a linear nest of up to ~ 20 cells (Ivanov (2006)) recorded a maximum of 28 cells with a mean of eight cells) (Fig. 9). A similar value of a maximum of 20 cells per nest was reported by Szentgyörgyi and Woyciechowski (2013) and a maximum of 16 cells was

reported by Seidelmann et al. (2016), but for a reed length of 19 cm (longer nesting materials were not tested in that study).
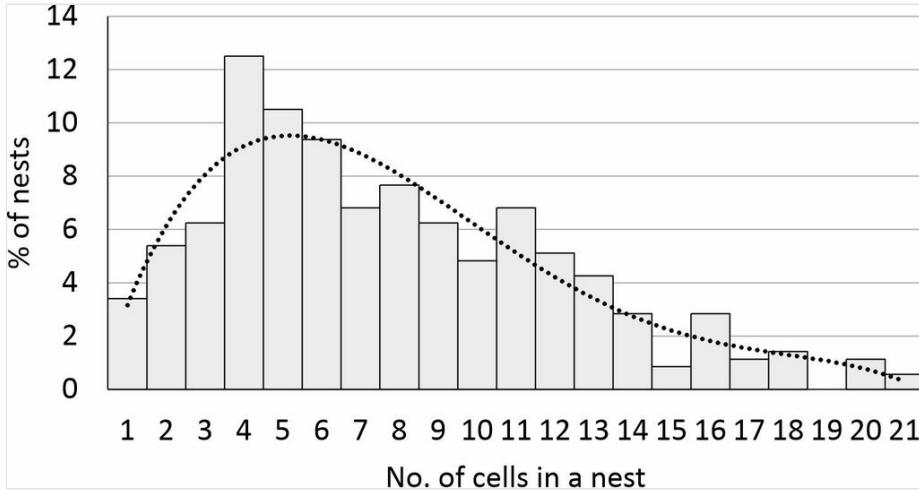

Figure 9. doi

The distribution of *O. bicornis* nests by number of cells, n = 188 nests were investigated (based on data from Ivanov (2006)).

Therefore, whenever a bee finds a patch with available nesting places, a nesting material (a reed, cavity etc.) of certain dimensions (length and diameter) is selected, which corresponds with a certain number of constructed cells. In general, the longer and wider the nesting material, the more cells can be constructed (Raw 1972, Seidelmann et al. 2016). In addition, according to Seidelmann et al. (2010), smaller bees produce fewer cells than larger bees if the nesting material of the same length (~ 15 cm) is offered (difference of ~ 3 cells). Additionally, bees tend to select better nesting materials (offering more space for new cells) at the beginning of their activity. Therefore, consecutive nests of the same bee tend to be smaller and smaller, i.e. consisting of fewer cells (Ivanov 2006, Giejdasz et al. 2016).

Implementation in the model

In the model, the minimum duration of pre-nesting will be set to 2 days with good weather conditions allowing for *O. bicornis* flying (flying conditions), that is, almost no rain (daily sum of precipitation < 0.1 mm) and no strong wind (i.e. wind speed < 8 m/s) and mean daily temperatures > 13°C (Bąk et al. 2003). This is because bad weather conditions do not allow for flying and feeding and will extend this period.

In the model, the nest will be defined as a linear structure of suitable diameter to allow the construction of *O. bicornis* cells. For simplicity, instead of describing nest size by two dimensions (length and diameter), we will characterise nest size through a possible number of cells that can be built within it.

After emergence, when a female bee finds a suitable nesting patch with free nesting places (see section "Use of resources"), it will select a nesting cavity of a certain size (allowing to build a certain number of cells). The number of planned cells (in optimal conditions) in the first nest will be randomly selected from a beta distribution $X \sim Beta\ (\alpha,\ \beta)$ with assumed parameters α = 1.8 and β = 5 with minimum and maximum values defined by the variables *OsmiaMinNoEggsInNest* and *OsmiaMaxNoEggsInNest* (Fig. 10) and further scaled by the bee-size class according to *BeeSizeScore1* parameter (see section "*Osmia mass*"). If, after rescaling, the number of cells planned is smaller than the minimum possible defined by the *OsmiaMinNoEggsInNest* variable, then it will be reset to the *OsmiaMinNoEggsInNest* value.
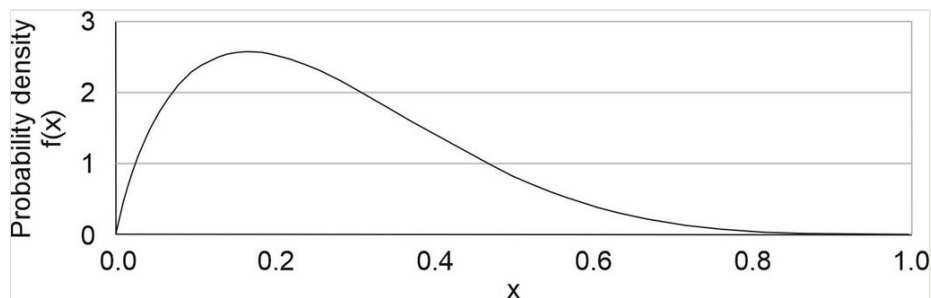

Figure 10. doi

The number of *O. bicornis* eggs in the first nest is defined as beta distribution $X \sim Beta\ (\alpha,\ \beta)$ with parameters α = 1.8 and β = 5.

The number of cells in consecutive nests will decrease by two cells per nest (*DecreaseStepNestSize*), following the study by Giejdasz et al. (2016). Furthermore, each time the nesting material is marked as occupied, the total number of nests available in a given habitat patch will decrease accordingly. In each nest, fertilised eggs (daughters) will always be laid first, followed by unfertilised ones (sons), according to the sex ratio, which depends on the *mass* of the mother bee and its reproductive age (see section "Reproduction").

Reproduction

Total reproductive potential

Seidelmann et al. (2010) found that, if nesting material of the same length is provided, smaller bees produce fewer cells than larger ones. This observation suggests that the total number of eggs a bee can lay in all colonised nests during its lifetime depends on its *mass*. The relationship can be drawn from the distribution provided by Giejdasz et al. (2016), in which the nesting activity of 17 females was observed (Fig. 11). However, bee sizes were not recorded in that study.
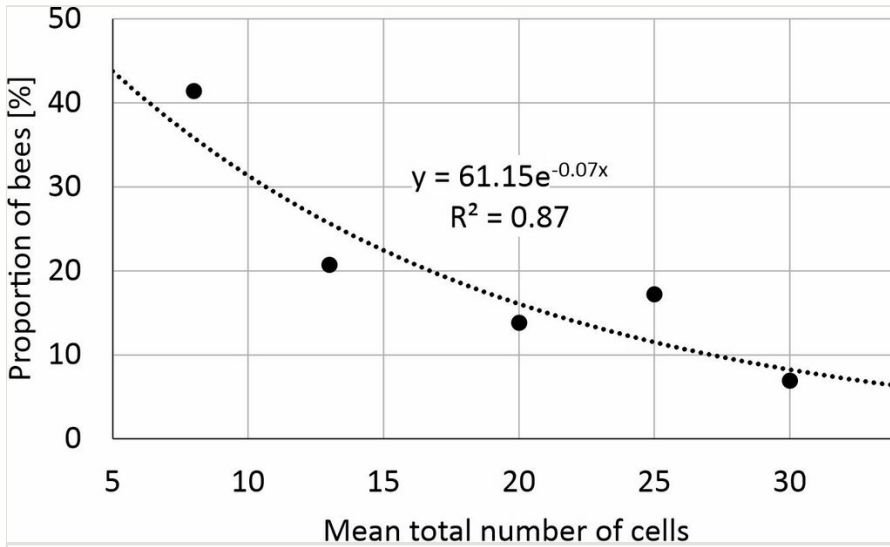
Figure 11. doi

Mean total number of cells produced by *O. bicornis* female (based on data from Giejdasz et al. (2016)).
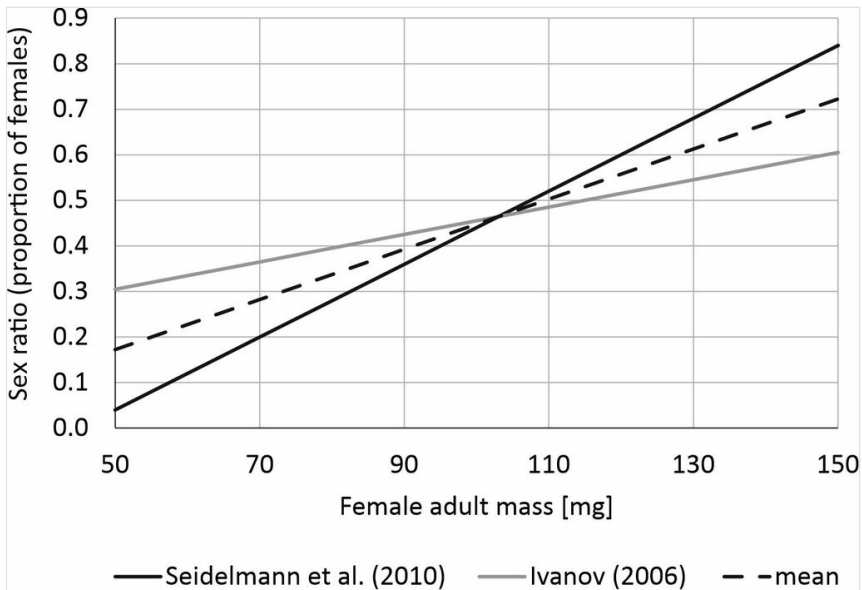
Sex ratio

The principle of risk spreading as well as the unpredictability of life expectancy, weather conditions and floral resources, favour a mixed-sex allocation in *O. bicornis*. The advantages of mixed nests force mother bees to shift the proportion of daughters and sons between different nests, as observed in the field, instead of a sex-assorted investment (Ivanov 2006, Seidelmann 2006). However, some nests (especially if narrow) only offer space for small cells and may only consist of males (Raw 1972, Seidelmann et al. 2016).

The probability of an egg being fertilised (female egg) depends on its position in the nest, i.e. non-fertilised eggs (sons) are laid closer to the nest entrance to lower the probability of female eggs (daughters) being attacked by parasites. The sex ratio (proportion of daughters) per nest depends on:

- Bee age, with later constructed nests having a higher probability of higher male share (Seidelmann 2006) (Fig. 12);
- Bee size, with larger bees having higher provisioning efficiency and, therefore, producing more daughters per nest (Ivanov 2006, Seidelmann et al. 2010) (Fig. 13);
- Nest diameter, with nesting materials of smaller diameter increasing the share of males (Raw 1972). According to Seidelmann et al. (2016), in nests with a diameter of 4 mm, daughter cells are constructed only exceptionally and the proportion of daughters increases with the nest diameter up to 8 mm, but not further;
- Nest length, inconsistent results.
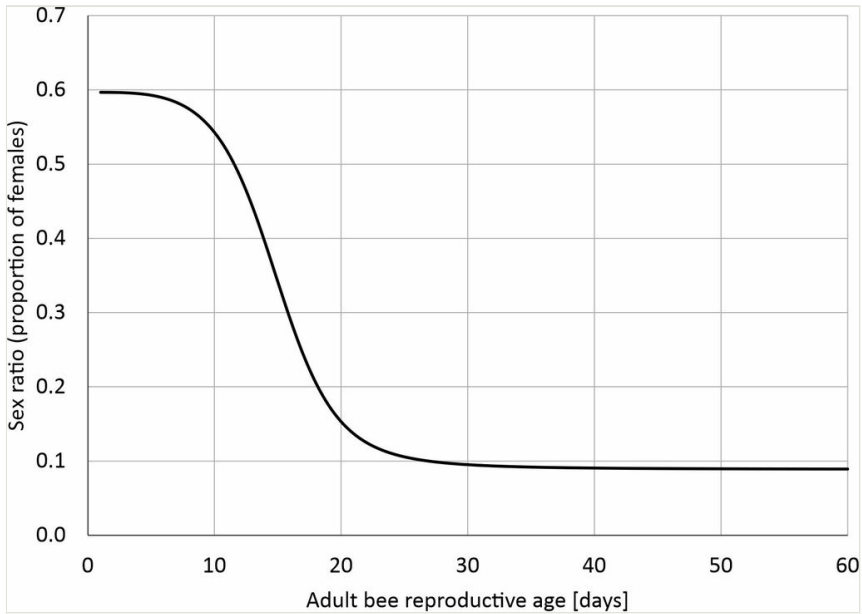
Figure 12. doi

Decline in the *O. bicornis* sex ratio (proportion of daughters per nest) in relation to the age of the mother (based on data from Seidelmann (2006)).

Figure 13. doi

Sex ratio (proportion of daughters) of *O. bicornis* per nest in relation to the mother's body *mass* according to Seidelmann et al. (2010) and Ivanov (2006).

Planned implementation in the model

In the model, the reproductive potential of the female will be characterised as the total number of eggs the bee can produce in her lifetime (property given to an adult female after emergence) and will depend on the bee *mass*. Therefore, we will assume that a given female of a *mass femaleAdultMass* can produce, on average, the following number of eggs per nest (see also Fig. 14A):
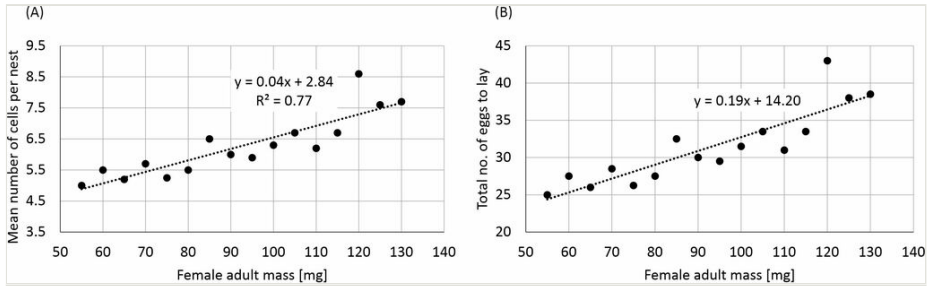

Figure 14. doi

Relationship between *O. bicornis* female body *mass* and mean number of cells per nest (data points read from Seidelmann et al. (2010)) (A) and assumed total number of eggs to lay for maximum number of five nests (B).

$$noEggsNest = 0.0371 \times femaleAdultMass + 2.8399(+/-3eggs)$$
(Eq. 15)

If we assume that a bee can colonise a maximum of *totalNestsPossible* nests in her lifetime, the maximum total number of eggs to lay will be defined as:

$$totalEggsPossible = totalNestsPossible \times noEggsNest \text{ (Eq. 16)}$$

For example, if *totalNestsPossible = 5*, then the maximum total number of eggs to lay increases with the *mass* of the mother bee, as shown in Fig. 14B.

In the model, we will combine the progeny sex ratio dependence on both the mother bee *mass* and reproductive age. The dependence on reproductive age (Fig. 12) will be modelled by a logistic curve with four parameters: inflection point, minimum value, maximum value and slope (Equation 17).

$$Logistic(x|x0, min, max, k) = \frac{min + (max - min)}{1 + exp(-k \times (x - x0))}$$
(Eq. 17)

We will consider that the dependence on body *mass* (Figure 13), showing that larger females produce more daughters, is valid for reproductive age zero. We will use a linear equation being a mean of those provided by Ivanov (2006) and Seidelmann et al. (2010):

$$sexRatio(age = 0, femaleAdultMass) = 0.0055 \times femaleAdultMass - 0.1025$$
(Eq. 18)

We will then create a family of logistic curves (Fig. 15), parameterised so that their maximum (which is reached at reproductive age zero) matches the *mass* dependence. When a female bee starts to build a nest, it will choose a sex ratio depending on its body *mass* at emergence and its current reproductive age according to Equation 19.
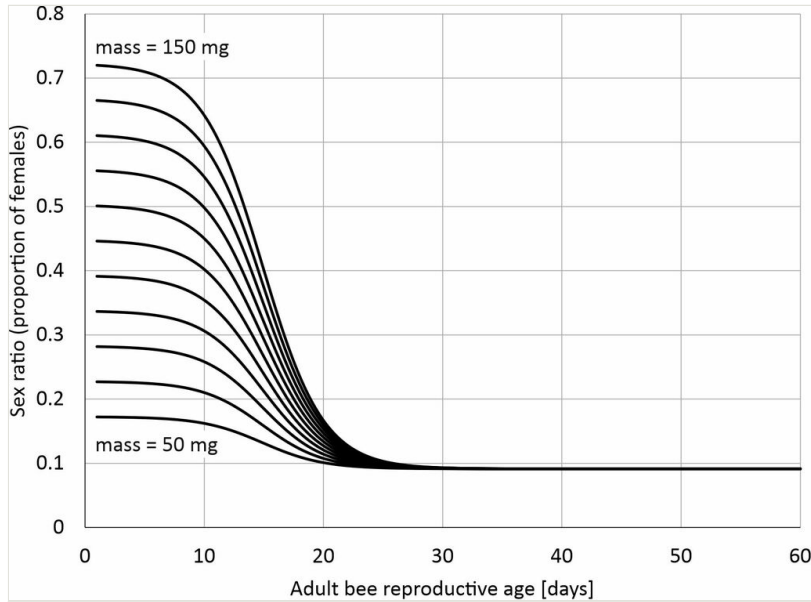
Figure 15. doi

Dependence of the *O. bicornis* nest sex ratio on mother bee *mass* and reproductive age. A family of logistic curves for the sex ratio is shown for mother bee masses from 50 to 150 mg with step of 10 mg.

$$sexRatio(age, femaleAdultMass) = 0.0914 + \frac{0.0055 \times femaleAdultMass - 0.1939}{1 + exp(0.3921 \times (x - 14.9026))}$$

(Eq. 19)

In the model, the family of logistic curves for the sex ratio will be calculated for bee sizes with a step defined by the *OsmiaAdultMassCategoryStep* variable. Then each mother bee will be linked with the proper curve using the *BeeSizeScore2* parameter (see section " *Osmia mass*").

Provisioning

Females provision brood cells with pollen and a comparatively low proportion of nectar (2-4%) (Maddocks and Paulus 1987, Strohm et al. 2002). After an egg is attached to the provision, the brood cell is sealed by a partition made of loam gathered by the female and brought to the nest in its mandibles.

The provisioning level differs between male and female progeny and is significantly higher for females. Provision *mass* is highly correlated with the cocoon *mass* of the offspring (and,

therefore, the body *mass* of the emerging bee). Under natural conditions, incompletely used provisions rarely occur in *O. bicornis* nests (Ivanov 2006, Seidelmann et al. 2010). However, according to Radmacher and Strohm (2010), the relationship between provision *mass* and cocoon *mass* and the amount of pollen remnants depends on the temperature under development (it could be substantial at prolonged extremely high temperatures > 30°C experienced by larva during development).

There is an optimal body size in both sexes of *O. bicornis*, i.e. bees scatter the size of their offspring around this optimum, irrespective of their own body size (Seidelmann et al. 2010). This optimum means that, although larger females generally produce larger offspring than smaller bees (both sexes), the larger females produce daughters that are, on average, smaller than themselves and smaller females produce daughters that are, on average, larger than themselves (Seidelmann et al. 2010). Similar results were obtained by Ivanov (2006), although the 'inversion' point is reached for smaller bees. Bees larger than ~ 74 mg started to produce daughters smaller than themselves, while in Seidelmann et al. (2010), those were bees larger than ~ 90 mg (Fig. 16).
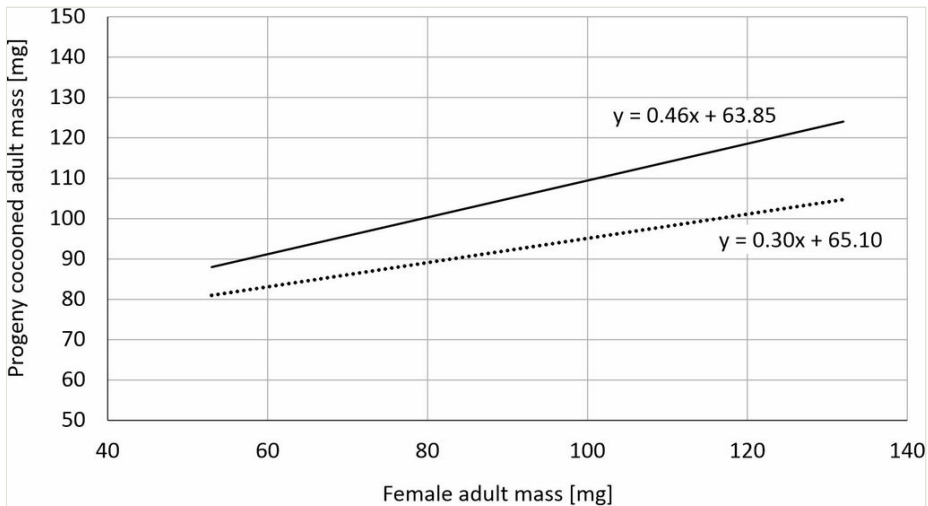
Figure 16. doi

Mean female progeny cocooned adult *mass* in relation to the mother bee *mass* according to Seidelmann et al. (2010) (black solid line) and Ivanov (2006) (black dashed line)

Therefore, under optimal/favourable conditions (unlimited pollen resources close by), there is a maximum amount of provision that a female is willing to provide to the nest and this depends on bee size. As bee provisioning efficiency decreases with bee age (Seidelmann 2006), the amount of pollen collected in consecutive cells in a linear nest should decrease (Ivanov 2006). This was deduced from the fact that the weight of cocoons with developing adults decreases in consecutive cells. The weight of female cocoons (and, therefore, collected pollen) decreases somewhat faster than that of male cocoons. The transition from the series of female cells to that of male cells is accompanied by an abrupt change in cocoon weight (and, therefore, the *mass* of provisions) (Ivanov 2006).

However, suppose the conditions are unfavourable (pollen resources are scarce, travel costs are high or weather conditions are bad for a longer time). In that case, food gathering is interrupted by the time norm and the egg is laid in an underloaded cell (Ivanov 2006). Prolonged provision times increase the risk of parasitism and force mothers to behave as smaller females (Seidelmann et al. 2010). Hence, under unfavourable conditions, other nesting parameters also change, i.e. females produce fewer cells per nest and in total and a shift in sex ratio towards the 'cheaper' sex is observed (females produce fewer daughters and more sons) (Ivanov 2006, Seidelmann et al. 2010).

Females of *O. bicornis* spend about 80% of the total time for cell preparation in collecting food (Raw 1972, Strohm et al. 2002). Only this effort is represented by the provision *mass* (or cocoon *mass*). The rest (20%) is the 'building costs' of the cell partitions and the nest plug.

In *O. bicornis*, the rate of provisioning of brood cells decreases with the age of the female (Seidelmann 2006) (Fig. 17), meaning that the older bee needs more time to provide the same amount of provision. In the model of Ulbrich and Seidelmann (2001), the parameter 'time necessary for complete construction' was not dependent on the size or age of the bees and was used as a habitat parameter. They assumed that it amounts to one day in rich habitats. Cell construction time is longer under unfavourable environmental conditions, which is related to the time norm described above.
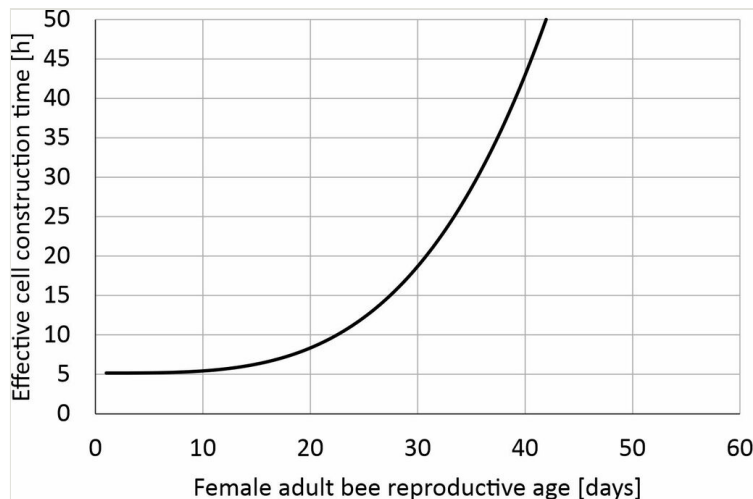

Figure 17. doi

Effective cell construction time depending on the age of the bee (based on Seidelmann (2006)).

Planned implementation in the model

After finding a suitable nesting location (see section "Nesting"), a bee will start to build a nest. Each bee will have a 'plan' to build *n* cells (based on their nesting plan; see section

"Nesting") with a given sex ratio (based on its age and *mass*; see section "Reproduction"), with a planned (or target) cocoon *mass* for each cell in the nest. Next, given the target cocoon *mass*, the amount of provision required will be given by Equations 5 and 6 in section "*Osmia mass*".

What is important, due to landscape (pollen resource availability), weather conditions, and other factors (e.g. death of bee or nest abandonment), the execution of the provisioning plan will not be guaranteed. Brood cells may be provisioned less than planned, the sex of the egg may be changed if provisions are too low and the total number of planned eggs per nest might be reduced.

Provisioning plan for the first female cell in the nest

The planned (target) cocoon *mass* for the first female in the nest will depend on the age and *mass* of the mother bee and we explain this next. The planned (target) cocoon *mass* of the following female and/or male cocoons in the nest will follow another pattern.

The dependence on the reproductive age of the mother bee will be a fitted logistic function, according to Seidelmann (2006), by combining the data for provisioning efficiency by age and the cocooned adult *mass* by provisioning efficiency. Similarly to the implementation of the sex ratio (see section "Reproduction"), the *mass* dependence will parameterise the maximum value of the logistic curve (i.e. the value for the reproductive age zero).

The *mass* dependence will be based on data from Seidelmann et al. (2010). The average *mass* of cocooned female (the average cocooned adult *mass* calculated for all female offspring produced by this bee in her lifetime) will be given by the following equation:

$$avgFemaleCocoonedMass = 0.46 \times femaleAdultMass + 63.85 (+/-5-7mg)$$
 (Eq. 20)

Based on Ivanov (2006), the maximum difference in cocooned adult masses produced by a bee in its lifetime will be set to 30 mg +/- 5 mg in the case of female offspring (*OsmiaLifetimeCocoonMassLoss*). Thus, the masses for the cocooned females at reproductive age zero, the maximum value parameter for the logistic curves, will be given by:

$$firstFemaleCocoonedMass = avgFemaleCocoonedMass + OsmiaLifetimeCocoonMassLoss/2$$
 (Eq. 21)

By combining Equations 20 and 21, we have:

$$firstFemaleCocoonedMass(age = 0, femaleAdultMass) = 0.46 \times femaleAdultMass + 63.85 + OsmiaLifetimeCocoonMassLoss/2 (+/-5-7mg)$$
 (Eq. 22)

The *mass* of cocooned offspring for the first female cell in the first nest will be calculated, based on the family of curves defined by Equation 23 (Fig. 18). Similarly to the sex ratio, the family of logistic curves for the *mass* of cocooned offspring will be calculated for bee sizes with a step defined by the *OsmiaAdultMassCategoryStep* variable. Then each mother bee will be linked with the correct curve through the *BeeSizeScore2* parameter.
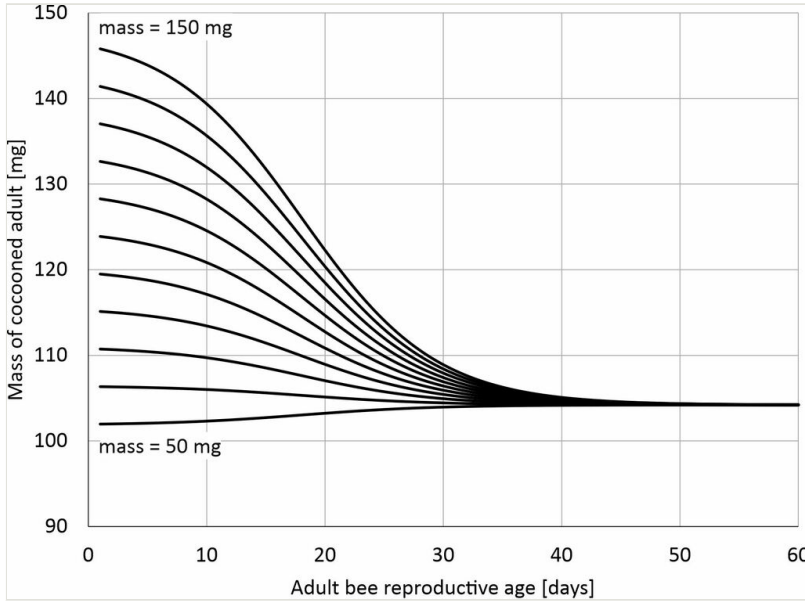
Figure 18. doi

Dependence of the female progeny cocooned adult *mass* on mother bee *mass* and reproductive age. A family of logistic curves for the *mass* of cocooned adult is shown for mother bee masses from 50 to 150 mg with a step of 10 mg.

$$firstFemaleCocoonedMass(age, femaleAdultMass) = 104.1982 + \frac{0.46 \times femaleAdultMass - 168.0482}{1 + exp(0.1769 \times (x - 18.0409))}$$

(Eq. 23)

The *mass* of cocooned offspring will be recalculated to the *mass* of provisions, based on Equation 5 (see section "*Osmia mass*").

Provisioning plan for the following cells in the nest

In a given nest, the *mass* of female cocooned offspring in consecutive cells will decrease at a fixed rate. Furthermore, based on Ivanov (2006), we assume that the difference between the maximum and minimum female cocooned offspring (the first and last cell with female offspring) will be constant in all nests and equal to 15 mg +/- 5 mg (*Osmia NestCocoonMassLoss*).

The total number of cells and sex ratio planned in the nest will be known from the nesting plan (see section "Reproduction"). The *mass* of the first female cocooned offspring will be calculated from the equations corresponding to Figure 19. The *mass* of the following female cocooned offspring will be calculated as follows:

$$femaleCocoonedMass[i] = femaleCocoonedMass[i - 1] - \frac{OsmiaNestCocoonMassLoss}{noFemaleCocoons}$$

(Eq. 24)

Regarding male cocooned offspring, we assume that there is a common minimum amount of provision needed for them (regardless of the order of nest and cell in a nest), defined by the variable *MaleMinTargetProvissionMass*.

Time and habitat conditioning – deviations from the provisioning plan

All the above will represent the 'plan' of the bee. It can be reached only in optimal (favourable) environmental conditions, i.e. if there are no restrictions on floral (pollen) resources around the nest and weather conditions allow for constant provisioning. Therefore, we assume there will be a certain minimum effective cell construction time, t_{min} and a maximum acceptable cell construction time, t_{max}. This maximum is because the longer the cell is open (while the bee is provisioning), the higher the risk of parasitism (Seidelmann 2006). We assume that the minimum effective cell construction time, t_{min}, defined as the minimum number of daylight hours with flying conditions, will be calculated, based on Seidelmann (2006) as a parameter dependent on bee age. For adult female bees of up to 14 days of age, the effective cell construction time ranges between 5 and 6 h (similar values were obtained by other authors, see, for example, Strohm et al. (2002)), which, under good weather conditions and in good habitat, can be reached in one day. We assume that the maximum acceptable cell construction time t_{max} will be defined as the time associated with the risk of provisioning at the level of 0.5, that is, according to Seidelmann (2006), equal to 0.5/0.022 = 22.7 h (~ 4 days).

If weather conditions allow, the bee will gather a certain amount of provision per day depending on the availability of food resources around the nest (see section "Use of resources"). Under optimal environmental conditions (enough pollen available in the proximity of the nest, good weather), the bee can fulfil her provisioning plan in t_{min}, that is, a maximum provision can be gathered in minimum time. However, if the floral resources are suboptimal, the amount of provision possible to collect in t_{min} will be smaller than the planned maximum and the offspring produced will be smaller. In such a case, the bee will continue provisioning the same cell (but it will increase the risk of parasitism) until:

1.   the maximum acceptable cell construction time t_{max} is reached or
2.   the provisioning planned for the egg is achieved.

In the case of the female progeny, if the stopping rule (1) is triggered before the stopping rule (2), then even if the provisioning plan has not been achieved, the mother bee will still lay a female egg if the amount of provision is above a defined threshold for female eggs. If not, then there will be a change in plan and a male egg will be laid (and the bee will continue to lay only male eggs afterwards for this nest attempt). If the provision is too small, even for a male egg, the current nest location will be given up. The procedure will continue for the next cells, with the amount of provisioning decreasing slightly for consecutive cells of daughters and sons and will be finished after the planned number of cells for this nest is reached. The bee will then start building another nest, following the same rules, but with a new 'plan' (i.e. number of eggs, sex ratio, amount of provision in each cell).

Weather will influence this plan, but only in such a way that, when the weather is bad (too cold, too rainy or too windy), the bee will have to wait in the nest and cannot provision (but the risk of parasitism will not increase as the bee stays in the nest and protects it).

Mortality

Mortality of the egg-to-pupa stages

Mortality at different developmental stages of *O. bicornis* in both natural and laboratory conditions was investigated by Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016). Radmacher and Strohm (2011) only differentiated between egg-to-cocoon, prepupa and pupa stages when investigating developmental mortalities (i.e. mortalities were not measured separately for egg and larva stages). In natural conditions (bees reared in an observation hut near the botanical garden of the University of Regensburg, Germany), the egg-to-cocoon mortality was 9.1%, while all bees survived through the prepupa and pupa stages. Giejdasz and Fliszkiewicz (2016) investigated mortalities separately for egg, feeding larva and spinning larva stages and together for prepupa and pupa stages. In natural conditions (bees reared in an observation hut in the dendrological garden of the Poznań University of Life Sciences, Poland), the highest mortality was observed in the egg stage (20.3%), while, for the larva stage, it was 12.6%. Similarly to Radmacher and Strohm (2011), almost all bees survived (99.6%) through the prepupa and pupa stages. The authors did not discuss the very high mortality at the egg stage. However, in the lab experiment by Sedivy et al. (2011) where egg hatching and larval development took place at fluctuating temperatures (25°C for 16 h followed by a gradual reduction of temperature to 10°C within 4 h, followed by a gradual increase back to 25°C within another 4 h), the mortality of the eggs and larvae were at a similar level (16.2% and 9.7%, respectively). Furthermore, Sedivy et al. (2011) and Bukovinszky et al. (2017) showed that larval survival could vary depending on the pollen diet.

Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016) also investigated the mortality rates of *O. bicornis* in relation to different temperature regimes. Radmacher and Strohm (2011), who investigated seven different regimes (three constant temperatures: 17.5°C, 22.5°C and 27.5°C and three fluctuating temperature regimes: 10–25°C, 15–30°C and 20–35°C), found that the egg-to-cocoon mortality and pupal mortality were not influenced by either temperature level or temperature fluctuations, while prepupal mortality was affected by temperature fluctuations, but not temperature level. Importantly, egg-to-cocoon mortality at a constant temperature of 17.5°C was higher than in the fluctuating temperature regime with the same mean temperature (9.1% vs. 5.2%). In contrast, the opposite was true when comparing mortality for constant temperatures of 22.5 and 27.5°C with fluctuating temperature regimes of the same mean temperatures (1.3% vs. 10.5% and 1.3% vs. 5.2%, respectively). Mortalities of the prepupa and pupa stages at constant temperatures were equal or close to zero.

Mortality rates of different developmental stages investigated by Giejdasz and Fliszkiewicz (2016) at three constant temperatures (20.0°C, 25.0°C and 30.0°C) were also generally not

related to temperature, although bees were more prone to die at the feeding larval stage. As in other studies, mortality in the prepupa and pupa stages was very low (≤ 1.5%). Very high mortality was observed in the egg stage at 25°C (24.7% compared to 6.3% and 6.9% at 20°C and 30°C, respectively), but according to K. Giejdasz (personal communication), mortalities observed at the egg stage are very uncertain as eggs are very sensitive to any disturbances and improper handling.

Both Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016) found no clear relationship between mortality and temperature, making it difficult to define optimal thermal windows for the developmental stages of *O. bicornis*. However, McKinney et al. (2017) showed that such thermal windows exist for *O. cornifrons* (population managed at the West Virginia University Organic Farm in Morgantown, West Virginia, USA) and they are different for eggs and larvae. While 100% of eggs survived at 13, 21 and 29°C and none at 5, 37 and 45°C, larvae survived only at 21 and 29°C, with 88.5% and 45.5% survival, respectively. The slightly different thermal windows for eggs and larvae were suggested by K. Giejdasz (personal communication) also for *O. bicornis*. Furthermore, the results provided by Bosch and Kemp (2000) for *O. lignaria* (from North Loga, Utah, USA) allow one to relate egg to adult developmental mortality to temperature (only constant temperatures were investigated; Fig. 19). Their work confirmed the existence of a similar thermal window for the development of this species (between ~13 and 37°C); this suggests that Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016) did not investigate all critical temperatures for *O. bicornis*.

(A) Developmental mortality [%] vs Temperature; $y = 0.6008x^2 - 29.4322x + 375.5501$, $R^2 = 0.9184$

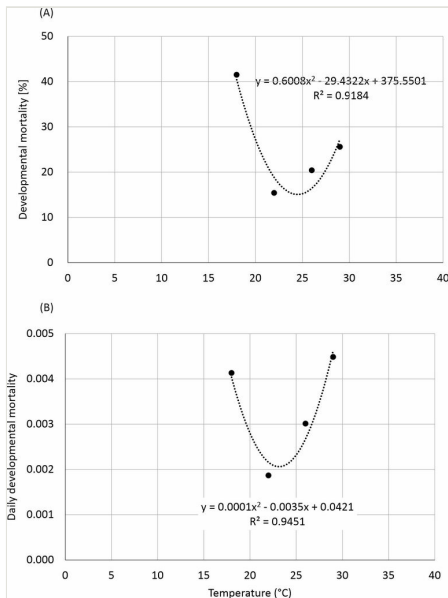(B) Daily developmental mortality vs Temperature (°C); $y = 0.0001x^2 - 0.0035x + 0.0421$, $R^2 = 0.9451$

Figure 19. doi

Developmental (A) and daily developmental (B) mortalities at different constant temperatures measured for the whole developmental period (from egg to adult) for *O. lignaria* (based on Bosch and Kemp (2000)).

Overwintering mortality

Overwintering temperatures (temperatures during diapause) do not influence overwintering mortality (Bosch and Kemp 2004, Fründ et al. 2013). However, the survival of solitary bees depends on the duration of the pre-wintering and wintering period, as exposure to a long period of wintering temperatures is required for diapause completion and emergence in the following spring. The longer the pre-wintering period with higher temperatures and the shorter the wintering period, the lower the overall winter survival (Bosch and Kemp 2004, Sgolastra et al. 2011).

Maximum survival is obtained for individuals pre-wintered for short to intermediate (15–30 days) periods (Bosch and Kemp 2004, Bosch et al. 2010, Sgolastra et al. 2011). Individuals pre-wintered for longer periods (45 – 80 days) maintain low respiration rates (~ 0.1 ml O_2/ g·h), but rapidly lose fat and, in consequence, body *mass* (0.2–0.4 mg/day). These individuals are less likely to survive winter and are less vigorous at emergence than individuals pre-wintered for 15–30 days (Bosch et al. 2008).

Background mortality outside the nest

Assessing the background mortality of *O. bicornis* outside the nest is difficult. According to Giejdasz et al. (2016), the daily background mortality rate for an adult *O. bicornis* female outside the nest is 0.02. The value comes from analysing the Kaplan-Meier survival curve for *O. bicornis* female adults developed under natural conditions, but observed in the laboratory after emergence. A survival probability of 0.5 was found for 34 days, i.e. 0.98^{34} =0.5. Under laboratory conditions, the survival probability of 0.5 was found for 20 days at 25°C and 30°C and 22 days at a temperature of 20°C. Thus, there are higher daily background mortality rates for an adult *O. bicornis* female outside than inside the nest, of 0.035 and 0.03, respectively.

Planned implementation in the model

Mortality of the egg-to-pupa stages

As all studies suggest that mortalities are very low in the prepupa and pupa stages and independent of temperature treatment, we will assume a constant daily mortality rate for these stages in the model. These being the mean of the results obtained by Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016), which is 0.003.

Regarding mortality at earlier developmental stages, we will not differentiate between egg and larva, but rather define mortality for the egg to cocoon. As there are not enough data for *O. bicornis* to assume temperature dependence, we will assume a constant daily mortality rate. This daily constant is defined as the mortality experienced by bees in a fluctuating temperature regime of 10-25°C in the study by Radmacher and Strohm (2011), which is 0.0014. This temperature regime seems to be the one that bees are likely to experience in Poland and Germany.

We do not plan to assume temperature-dependent egg-to-cocoon mortality, as this would require substantial extrapolation and manipulation of existing data (Fig. 20).
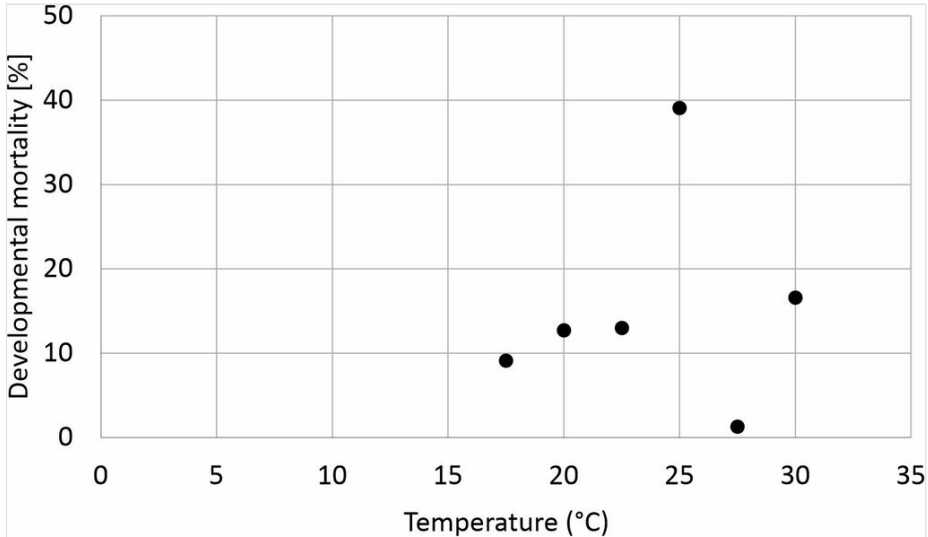
Figure 20. doi

Developmental mortalities at different constant temperatures measured for the egg to cocoon for *O. bicornis*, based on Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016).

Overwintering mortality

Although it has been shown that the duration of both the pre-wintering and the wintering periods can influence overwintering mortality in *Osmia* spp. (Bosch and Kemp 2004), these relationships were investigated in European *Osmia* bees only for *O. cornuta* flying in March-April in La Garrotxa (NE Spain), i.e. much earlier than *O. bicornis* in central Europe (April – early June). Therefore, we will define overwintering mortality only in relation to pre-wintering conditions, based on results obtained for *O. lignaria* reared in natural conditions in North Ogden, Utah, USA, flying in April – May (Sgolastra et al. 2011). Sgolastra et al. (2011) related overwintering mortalities of *O. lignaria* males to degree days accumulation over the pre-wintering period (Fig. 21). Degree days accumulation (*DD*) was calculated using 15°C as the baseline temperature, i.e. $DD = \Sigma(Tavg - T_0)$. As no relevant field data are available for females, we will use the linear relationship for males, assuming that it is applicable to both sexes. We will calculate the pre-wintering degree days accumulation, *DD_prewinter*, with a baseline temperature T_0 = 15°C and only for days when *Tavg – T0* ≥ *0*, i.e.:

$$overwintering Mortality = 0.05 \times \sum (DD\_prewinter) - 4.63$$
(Eq. 25)

The duration of the pre-wintering period will be defined according to the section "Overwintering". The overwintering mortality test will be applied only once, at the end of the overwintering period (before emergence).
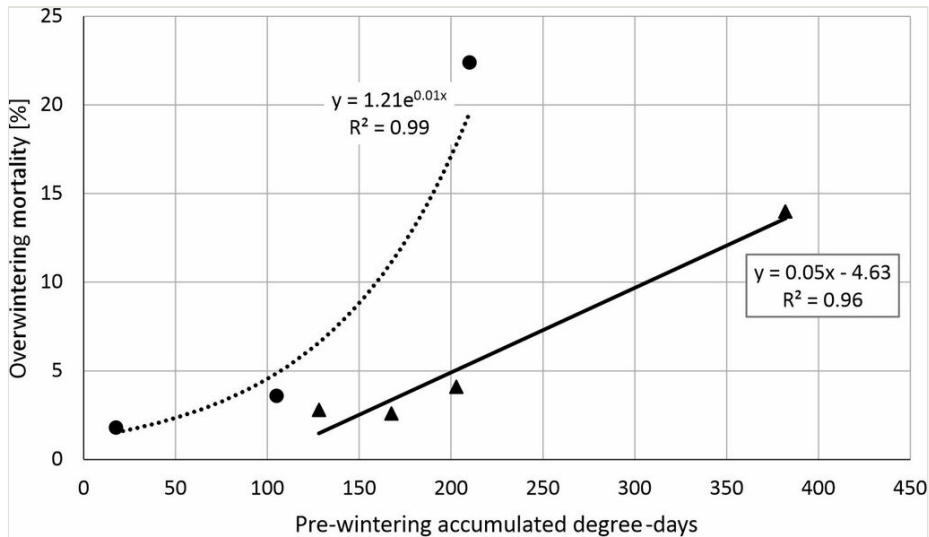
Figure 21. doi

Overwintering mortality of *O. lignaria* males (reared in natural conditions; black triangles) and females (reared in lab conditions; black dots) in relation to accumulated degree days during the over-wintering period (based on Sgolastra et al. (2011)).

Background mortality outside the nest

We will define the daily background mortality rate for an adult *O. bicornis* female outside the nest equal to 0.02.

Parasitism

Parasites attacking *O. bicornis* and bees of the *Osmia* genus, in general, can be divided into cleptoparasites and parasitoids.

Cleptoparasites lay eggs in bee nests and their larvae consume the host bee's food provision and sometimes the host egg or larva. Within this group, the most common in *O. bicornis* nests are:

- *Cacoxenus indagator* Loew (Diptera, Drosophilidae) is a small drosophilid fly reported as the most significant organism restricting populations of *O. bicornis* (and also *O. cornuta*) in central Europe (Seidelmann 2006, Fliszkiewicz et al. 2012, Zajdel et al. 2016) and southeast Europe (Krunić et al. 2005). *C. indagator* lays eggs within bee nests during the provisioning phase (when the cell is open) and its larvae consume the food provision. Adult *C. indagator* females wait at the side of the bee's nest and when a bee leaves, the fly hurriedly enters it, lays an egg on the

pollen provision, rapidly departs and awaits the next opportunity (Krunić et al. 2005). The degree of harm of *C. indagator* depends on the number of larvae in the nest cell. If there are only a few (2-3), the bee larva can still develop alongside them and spin a cocoon. The presence of 2-3 *C. indagator* larvae can influence bee larva development and decrease cocoon size (Krunić et al. 2005). However, in the experiment conducted by Zajdel et al. (2016), no such effect was found, which was partly explained by the amount of pollen available in cells, i.e. under good foraging conditions, the provision *mass* could be so large that the presence of 2-3 larvae of this cleptoparasite in the cell does not impair the normal development of the bee larva. However, when there are many larvae of *C. indagator* (several or more), the bee larva does not have the chance to develop. When present in large numbers, *C. indagator* larvae can perforate the wall of the neighbouring cell or several cells in a row and also consume their contents. The level of infestation depends on the synchronisation between the phenology of *O. bicornis* and *C. indagator*, that is, if bees are able to complete their activity (spin a cocoon) before hatching of *C. indagator*, the level of infestation is low;

- *Chaetodactylus osmiae* Dufour (Acarina, Chaetodactylidae) is a Hypoderatidae mite distributed throughout Europe, commonly found in nests of many European species of solitary bees. The migratory hypopi is transported to a cell by the bees via phoresy; therefore, mite parasitism cannot be reduced by shortening the time away from the nest. When transported into a host's cell, a mobile hypopus continues its development cycle. Mites eat pollen and nectar from the cell, preventing larvae from developing. Some mites of the genus *Chaetodactylus* have also been reported to sometimes consume the contents of bee eggs and even certain later stages of development, in addition to pollen and nectar. Male and female bees during emergence from the nest pass through cells with many mobile mite hypopi, which they carry in sometimes great numbers. Due to high fertility, *Ch. osmiae* can be a real threat to bee food reserves. A succession of rainy summers without dry periods or extremely high temperatures favours the *mass* development of hypopi in cells, resulting in significant increases in infestation in bee populations (Krunić et al. 2005);

- Sapygid wasp (Hymenoptera, Sapygidae) females enter mason bee nests after female bees have finished provisioning a cell and have laid an egg. Sapygids oviposit into newly-completed cells, either before the cell wall is completed or while the wall is still malleable. In the latter case, they oviposit through the cell wall. The sapygid larva consumes the yet unhatched bee egg and the food provision within the cell (Groulx and Forrest 2018). *Sapyga quinquepunctata (L.)* was found in *O. bicornis* nests by Fliszkiewicz et al. (2012);

- *Chrysis ignita* Loew (Hymenoptera, Chrysididae) is a wasp found in Europe. It lays eggs in nests of other wasp species and mason bees. It was found in nests of *O. bicornis* by, for example, Fliszkiewicz et al. (2012). *C. ignita* larva feeds on reserves of food gathered earlier by the host. They can often infest several successive cells in the nest of solitary bees.

Parasitoids lay eggs within or adjacent to bee larvae or eggs and their larvae develop and consume the bee larva as a host. The most common parasitoids of this group are the following:

- *Anthrax anthrax* Schrank (Diptera, Bombyliidae) is a common parasite of *O. bicornis* nests, especially in Germany, Poland and Italy (Krunić et al. 2005, Seidelmann 2006, Fliszkiewicz et al. 2012). This bombylid fly lays its eggs in open cells during the provisioning phase. Females of *A. anthrax*, hovering in front of solitary bee nests, shoot an egg into the hole entrance. The first instar larva of *A. anthrax* is called planidium and is characterised by high mobility so that it reaches the bee pollen provision before the cell is sealed. Planidium parasites the bee after the larva spins a cocoon (Felicioli et al. 2017). It is not clear if the planidium could pass through the mud partitions (Krunić et al. 2005). The damage caused by this fly is direct and/or indirect. The direct damage is that each fly planidium kills the *Osmia* larva, usually in the inner part of the nest containing the future female bees. The indirect damage is caused by armed pupae that start migrating towards the nest entrance during August (50% of the fly population). On their way, they crush all cocoons containing bee larvae, killing them and causing very high mortality in the *Osmia* populations. In this case, *A. anthrax* could be considered a nest destroyer (Felicioli et al. 2017);
- *Monodontomerus obscurus* Westwood (Hymenoptera, Torymidae) is a wasp distributed in northern Europe, but also found in *Osmia* nests in Poland (Fliszkiewicz et al. 2012). The *M. obscurus* female perforates with its ovipositor the reed nest, the cocoon and integument of the host larvae, injects a paralysing fluid and then lays several eggs on or near the mature bee larva. The larva of *M. obscurus* feeds on the prepupae or white pupae of the bee.

Most cleptoparasites and parasitoids represent the type of open-cell parasitism. Only the cleptoparasite mite *Ch. osmiae* and the parasitoid wasp *M. obscurus* are important *O. bicornis* parasites that do not belong to this group.

Several factors affect parasitism rates in the genus *Osmia*. Seidelmann (2006) found that the risk of open-cell parasitism in *O. bicornis* nests (by *A. anthrax* and *C. indagator*) decreases towards the inner part of the nest. However, the rate of parasitism decrease is not uniform throughout the nests. In the study by Groulx and Forrest (2018), the last (outermost) cell in the nests of the mason bees, *Osmia iridis*, *Osmia tersula*, *Osmia tristella* and *Osmia montana* in Colorado, USA, was significantly more often affected by Sapygid wasps than were inner nest cells. The authors suggest that this can be explained by the fact that bees may terminate nests earlier than normal after a brood parasite attack. However, this would mean that bees can sense the presence of Sapygid wasps inside the nest. On the other hand, Seidelmann (2006) reported that females of *C. indagator* and *A. anthrax* inspect host nests randomly and do not guard parasitised nests or mark nest entrances. It was also shown that the risk of open-cell parasitism by *A. antrax* and *C. indagator* increases with cell provisioning time; the longer the cell is open, the higher the risk. As the provisioning time increases with bee age, so does the risk of open-cell parasitism (Seidelmann 2006).

Fliszkiewicz et al. (2012) found that the rate of parasitism in *O. bicornis* nests was significantly higher in mixed forest habitats (mostly with coniferous trees with relatively numerous bushes in lower layers and herbaceous plants in the understorey and groundcover) than in hay meadow and orchard (9.5% compared to 5.9% and 2.4%, respectively), but the types of parasites recorded were similar. Goodell (2003) investigated the influence of resource availability on the risk of parasitism by the cleptoparasitic wasp *Sapyga centrata* in *Osmia pumila*. She found a 15-fold higher probability of parasitism in cages with sparse blooms than in those with rich blooms. Furthermore, the risk of parasitism in open cells is correlated with the provisioning time (Seidelmann 2006), which means that – if an adequate food base is ensured – mason bee females do not leave the nest for long, preventing females of cleptoparasites from laying more than a couple of eggs (Zajdel et al. 2016).

Groulx and Forrest (2018) found positively density-dependent parasitism in populations of the mason bees *O. iridis*, *O. tersula*, *O. tristella* and *O. montana* in Colorado, USA, i.e. as the number of active bees in the nest increased, the proportion of nest cells parasitised by Sapygid wasps increased too (from 4.2% for one active bee to 25.0% for four active bees in the 2014 dataset and from 18.1% to 25.0%, respectively in the combined 2013-2015 dataset). However, in the study by Felicioli et al. (2017), parasitism rates were density independent in the first study year, positively density-dependent in the second year and negatively density-dependent during consecutive years. The authors suggest that high densities of *O. bicornis* females foraging in large populations/aggregations may reduce the success of *C. indagator* (the main parasite in the studied bee populations), thereby explaining the inverse density-dependent rates of parasitism.

Planned implementation in the model

In the model, we will consider only open-cell parasitism. Its probability will depend on the time the cell is open according to the equation provided by Seidelmann (2006):

$$openCellParasitismProb = 0.022 \times timeCellOpen[h]$$ (Eq. 26)

If the cell is parasitised, it will be in the form of cleptoparasitism by flies and wasps (e.g. *C. indagator* drosophilid fly and Sapygid wasps) or parasitism by flies (e.g. *A. anthrax* bombylid fly), with a given probability defined by the *OsmiaBombylidProb* variable.

Parasitism by flies will influence the offspring in two ways:

1.   directly, by parasitising on the bee larva that causes its death and
2.   indirectly, when the parasite is moving towards the nest entrance killing all bee larvae as it leaves the nest.

In the case of cleptoparasitism, we know that the influence of cleptoparasites on offspring depends on the number of eggs laid in the host cell by the parasite and these do not always cause the death of the bee larvae, i.e. if only a few eggs are laid, the cleptoparasite larvae do not have to eat the entire bee provision. However, since, in most cases, the

number of cleptoparasite eggs is large enough to cause the removal of the entire or most of the bee supply, we will assume that if the cleptoparasite attacks the cell, it always results in the death of the bee larva.

We will not consider the influence of habitat on the probability of parasitism but we plan to add this impact in the next versions of the model development.

Use of resources

O. bicornis depends on both nesting and foraging habitats. It may use a wide range of natural nesting cavities, such as dry stems of hollow plants (e.g. the common reed), dead wood or even cavities in building walls or wooden fences. A five-year experimental study by Steffan-Dewenter and Schiele (2008) showed a steady increase in *O. bicornis* population size in response to the additional nesting resources, therefore, indicating that nesting sites are a limiting resource for local population size.

On the other hand, it has been suggested that food limitation is not common in *O. bicornis* at natural densities, which are far from their carrying capacity (Steffan-Dewenter and Schiele 2008, Everaars et al. 2011, Coudrain et al. 2016). Analysis of pollen from nests shows that *O. bicornis* can forage for pollen produced by a wide variety of plants (Raw 1974, Biliński and Teper 2004, Haider et al. 2014, Söderman et al. 2018, Bednarska et al. 2022). However, *O. bicornis* shows some seasonal preferences. Just after emergence, it collects pollen mainly from early flowering trees like *Acer* or *Quercus*, while shifting more towards herbaceous sources of pollen, such as *Ranunculus acris*, *Cirsium* spp. and *Papaver* spp., during summer (Coudrain et al. 2016, Persson et al. 2018, Bertrand et al. 2019, Splitt et al. 2021).

Planned implementation in the model

Evaluation of nesting resources

Nesting density will be provided as the number of nests available per 1 m^2 of each landscape element in the land-cover map. For each type of landscape element, the minimum and maximum nesting density will be defined and the actual nesting density of a landscape element will be driven from this range of values at the beginning of each simulation.

The minimum and maximum nesting density will be calculated, based on the cavity nesting suitability provided by Koh et al. (2016). The given suitability values will be recalculated to nesting density assuming that the suitability of 1 equals the maximum density, that is, if 1 m^2 of stems with hollows would be available (~ 100 cells are available). Furthermore, because the landscape units/habitat types analysed by Koh et al. (2016) were different from those used in ALMaSS, a necessary translation table will be applied (Table 5).

Table 5.

Minimum and maximum nesting density defined for different types of landscape elements (TOLE) of the land-cover map in ALMaSS, based on nesting suitability values for cavity-nesting bees provided by Koh et al. (2016).

Type of landscape element in ALMaSS (TOLE)	Habitat type (according to Koh et al. (2016))	Nesting suitability (according to Koh et al. (2016)) for cavity-nesting bees			Min nesting density [no of nests/m^2]	Max nesting density [no of nests/m^2]
		Mean	Low25	Upp75		
Building	-	-	-	-	0.00	0.00
UrbanNoVeg	Developed / High Intensity	0.14	0.00	0.15	0.01	15.39
UrbanVeg	Developed / Low Intensity	0.21	0.00	0.34	0.25	34.43
Garden	Developed / Open Space	0.24	0.01	0.41	0.67	41.42
AmenityGrass	-	-	-	-	0.00	0.00
RoadsideVerge	Grass	0.20	0.00	0.32	0.12	31.58
Parkland	Developed / Open Space	0.24	0.01	0.41	0.67	41.42
StoneWall	-	-	-	-	0.00	0.00
BuiltUpWithParkland	Developed / Low Intensity	0.21	0.00	0.34	0.25	34.43
UrbanPark	Developed / Open Space	0.24	0.01	0.41	0.67	41.42
Field	-	-	-	-	0.00	0.00
PermPastureTussocky	Pasture / Hay	0.25	0.02	0.41	2.13	41.48
PermPastureLowYield	Pasture / Hay	0.25	0.02	0.41	2.13	41.48
UnsprayedFieldMargin	Grass	0.20	0.00	0.32	0.12	31.58
PermanentSetaside	Grass	0.20	0.00	0.32	0.12	31.58
PermPasture	Pasture / Hay	0.25	0.02	0.41	2.13	41.48
DeciduousForest	Deciduous Forest	0.72	0.51	0.97	51.34	97.28
Copse	Shrubland	0.67	0.45	0.94	45.22	93.87
ConiferousForest	Christmas Trees	0.32	0.01	0.61	0.99	61.02
YoungForest	Shrubland	0.67	0.45	0.94	45.22	93.87
Orchard	Orchard	0.25	0.00	0.44	0.18	44.33
BareRock	-	-	-	-	0.00	0.00
OrchardBand	Orchard	0.25	0.00	0.44	0.18	44.33
MownGrass	Grass	0.20	0.00	0.32	0.12	31.58

Type of landscape element in ALMaSS (TOLE)	Habitat type (according to Koh et al. (2016))	Nesting suitability (according to Koh et al. (2016)) for cavity-nesting bees			Min nesting density [no of nests/m^2]	Max nesting density [no of nests/m^2]
		Mean	Low25	Upp75		
MixedForest	Mixed Forest	0.68	0.45	0.96	45.28	95.62
Scrub	Shrubland	0.67	0.45	0.94	45.22	93.87
PitDisused	Barren	0.08	0.00	0.09	0.05	9.40
Saltwater	Open Water	0.00	0.00	0.00	0.00	0.00
Freshwater	Open Water	0.00	0.00	0.00	0.00	0.00
Heath	Herbaceous Wetlands	0.15	0.00	0.19	0.04	18.64
Marsh	Wetlands	0.25	0.00	0.46	0.17	45.93
River	Open Water	0.00	0.00	0.00	0.00	0.00
RiversideTrees	Woody Wetlands	0.34	0.01	0.69	0.94	68.89
RiversidePlants	Wetlands	0.25	0.00	0.46	0.17	45.93
Coast	-	-	-	-	0.00	0.00
SandDune	-	-	-	-	0.00	0.00
NaturalGrassDry	Grassland Herbaceous	0.58	0.31	0.88	30.78	87.98
ActivePit	-	-	-	-	0.00	0.00
Railway	-	-	-	-	0.00	0.00
LargeRoad	-	-	-	-	0.00	0.00
SmallRoad	-	-	-	-	0.00	0.00
Track	-	-	-	-	0.00	0.00
Hedges	Shrubland	0.67	0.45	0.94	45.22	93.87
HedgeBank	Grass	0.20	0.00	0.32	0.12	31.58
BeetleBank	Grass	0.20	0.00	0.32	0.12	31.58
FieldBoundary	Grass	0.20	0.00	0.32	0.12	31.58
RoadsideSlope	Grass	0.20	0.00	0.32	0.12	31.58
MetalledPath	-	-	-	-	0.00	0.00
Carpark	-	-	-	-	0.00	0.00
Churchyard	Developed / Open Space	0.24	0.01	0.41	0.67	41.42
NaturalGrassWet	Grassland Herbaceous	0.58	0.31	0.88	30.78	87.98
Saltmarsh	-	-	-	-	0.00	0.00
Stream	-	-	-	-	0.00	0.00

Type of landscape element in ALMaSS (TOLE)	Habitat type (according to Koh et al. (2016))	Nesting suitability (according to Koh et al. (2016)) for cavity-nesting bees			Min nesting density [no of nests/m^2]	Max nesting density [no of nests/m^2]
		Mean	Low25	Upp75		
HeritageSite	-	-	-	-	0.00	0.00
Wasteland	Barren	-	-	-	0.05	9.40
UnknownGrass	Grass	0.20	0.00	0.32	0.12	31.58
WindTurbine	-	-	-	-	0.00	0.00
Pylon	-	-	-	-	0.00	0.00
IndividualTree	Mixed Forest	0.68	0.45	0.96	45.28	95.62
PlantNursery	-	-	-	-	0.00	0.00
Vildtager	Flowers	0.09	0.00	0.08	0.01	8.31
WoodyEnergyCrop	Tree Crops	0.37	0.02	0.73	1.54	72.78
WoodlandMargin	Shrubland	0.67	0.45	0.94	45.22	93.87
PermPastureTussockyWet	Pasture / Hay	0.25	0.02	0.41	2.13	41.48
Pond	Open Water	0.00	0.00	0.00	0.00	0.00
FishFarm	Open Water	0.00	0.00	0.00	0.00	0.00
RiverBed	Open Water	0.00	0.00	0.00	0.00	0.00
DrainageDitch	Grass	0.20	0.00	0.32	0.12	0.00
Canal	Open Water	0.00	0.00	0.00	0.00	0.00
RefuseSite	-	-	-	-	0.00	0.00
Fence	-	-	-	-	0.00	0.00
WaterBufferZone	Wetlands	0.25	0.00	0.46	0.17	45.93
Missing	-	-	-	-	0.00	0.00

Evaluation of food resources

We assume that adult bees are not limited by their food requirements; therefore, we will focus only on assessing pollen resources for offspring. We also assume that the model providing a spatially and temporally changing pattern of pollen resource density will be available as a part of the ALMaSS landscape model (it is currently under development). Thus, on each day of the simulation, a bee will be able to sample the landscape to obtain information on the amount of pollen produced in a given resource patch (in mg per m^2), taking into account only pollen produced by plants visited by *O. bicornis*. The plants that compose each habitat type will be divided into those used and not used by *O. bicornis* (i.e. qualitative approach based on literature and expert knowledge). In addition, competition from other pollinators will be modelled as a global decrease in floral resources available to *O. bicornis*.

Since the foraging patterns are not well known for *O. bicornis*, there is little information on which to base a search algorithm. It is clear, however, that *O. bicornis* makes an active choice of forage locations and it seems sensible to assume that they explore the area around the nest, likely with the efficiency decreasing with distance. To implement this, we suggest that we use a radial-spoke pattern of searching from the nest location. When the bee needs to find a forage location, it will search in eight directions (N, NE, E, SE, S; SW, W, NW) and select the best forage location encountered within the typical homing distance *r50* (see section "Foraging and dispersal"). Since the pattern is radial with the spokes evenly distributed, the chance of encountering a patch of pollen decreases with distance from the nest and the likelihood of encounters near the nest is very high. The bee will continue to forage from the patch found as long as the pollen return rate is high enough (threshold parameter, for example, 75%) and a new nest is not started. If either condition is triggered, a new search will be initiated. This algorithm does not map to any measurable biological parameters, except forage distance; hence the step size, acceptance level and frequency of search will need to be fitted.

Discussion

The *Osmia* model is based on a relatively large body of literature; however, many processes have uncertain parameter values and mechanisms. Information comes primarily from laboratory studies or studies using artificial nests to manage studied populations. In some cases, the data come from species other than *O. bicornis*. This means that some crucial information about the species is still missing. Important missing knowledge includes the actual population densities found in the field in different habitats and under other conditions, adult emergence time and reproductive success under natural conditions.

The problem expected to be encountered in the calibration is that the development times measured under constant laboratory conditions are very different from those experienced by the bees in the wild. In the field, temperatures fluctuate and are experienced differently by different nests with different locations (aspect, height, exposure). It is also still to be determined to what extent a nest itself may buffer natural ambient temperature fluctuations. The fluctuating temperatures are considered in the model through the input weather file. The weather input file consists of real daily weather data; thus, the development will be assessed, based on the mean daily temperature. However, there is a variation in temperature within the day, which is not considered in this version of the model. In future versions, we plan to implement hourly weather data, which are now available for Europe (Hersbach et al. 2023). A final, but important issue here is that we have planned for a simple degree-day model. However, a biophysical model (Sharpe and DeMichele 1977) is much more likely to represent the true picture. Unfortunately, insufficient data are available to parameterise this more complex model, but if possible, later, it would perform better under fluctuating temperatures. In addition, the degree-day models, based on laboratory data from Giejdasz and Wilkaniec (2002) and Radmacher and Strohm (2011) and Giejdasz and Fliszkiewicz (2016) suggest quite a high base temperature to calculate the transition threshold from egg to larva stage (13.8°C). This high estimated temperature may be

caused by the fact that the egg stage only lasts a few days and may be more difficult to measure precisely. Similarly, the studies on overwintering mortality and time of emergence were carried out in constant temperature conditions. After overwintering, bees were transferred from low (e.g. 4°C) to relatively high (e.g. 12-17°C) temperatures in quite a short time. In natural conditions, temperature changes experienced by bees in the nest are not so abrupt.

The timing of adult emergence in *Osmia* spp. depends on the overwintering conditions. Longer overwintering periods result in shorter emergence periods (Bosch and Blas 1994, Bosch and Kemp 2003, Giejdasz and Wasielewski 2017). This mechanism can be used to manipulate bee emergence in such a way as to synchronise it with tree flowering in orchards to maximise pollination services. Emergence time also depends on overwintering temperatures; i.e. the warmer the winter, the shorter the emergence period (Bosch and Kemp 2003, Bosch and Kemp 2004, Fründ et al. 2013). Although these mechanisms are well documented (also for *O. bicornis*), they have been studied under laboratory conditions with predefined overwintering temperature regimes and incubation start dates. The requirements for post-diapause onset under natural conditions are poorly studied and, therefore, challenging to parameterise. To relate the duration of the emergence period to overwintering temperatures, we plan to use the equation provided by Fründ et al. (2013) for *O. bicornis*. To follow their study's experimental design, we propose using 1 March as the start of the incubation period. However, we are aware that this is an artificial condition that should be tested during the calibration of the model.

Bee *mass* loss during overwintering is not included in this version of the model. As Fründ et al. (2013) reported only a slight reduction in *mass* (up to ~ 3%) for *O. bicornis* during overwintering, we assume that *mass* loss during overwintering is independent of temperature and, therefore, a linear relationship between the *mass* of the cocooned female and the *mass* of the adult female can be accepted. However, this assumption requires further verification as Sgolastra et al. (2011) showed a dependence of *mass* loss during overwintering on pre-wintering conditions for *O. lignaria*. They also reported differences in *mass* loss rates between adult diapause phases. This is an interesting issue that could be further investigated in future versions of our model once more data for *O. bicornis* are available.

Our model assumes a positive relationship between bee *mass* and fecundity (total number of offspring produced and the sex ratio), following studies on *O. bicornis* by Ivanov (2006) and Seidelmann et al. (2010). The review of studies on parental investment in solitary bees and wasps by Bosch and Vicens (2006) shows inconsistent results but suggests a stronger relationship between body *mass* and reproductive success in wasps than in solitary bees. The later published studies by Ivanov (2006) and Seidelmann et al. (2010) were not included in this review, nor were any studies on *O. bicornis*. Therefore, until new evidence on *O. bicornis* becomes available, we believe that following the results of Ivanov (2006) and Seidelmann et al. (2010) is a reasonable approach.

As the available data for *Osmia* spp. are mainly from laboratory studies or artificial nests, we need more information on population density regulation mechanisms. We know that

relying on expert opinion to set the habitat-related nesting densities is the key driver since the model does not include other regulating feedback. We do not expect the food limitation or the weather to act that way. One key aspect of the density-dependence response of *Osmia* spp. in natural populations is related to parasitoids. The relationship is, however, complicated. Therefore, we decided to defer the development of a full parasitoid model until a later model version. This is because the response picture varies in time and space (see section "Parasitism") and would require a separate modelling study to untangle the relationships with the parasitoid community. Theoretically, the parasitism rate might be positively related to the density of nests. Still, Groulx and Forrest (2018) showed that *O. iridis*, *O. tersula*, *O. tristella* and *O. montana* in Colorado, USA, do not exhibit the behaviour to avoid nesting near each other. In fact, the opposite tendency, i.e. to create aggregations, was found in *O. lignaria* by Torchio (1984) in the agricultural landscape. Therefore, it is possible that *O. bicornis* shares this characteristic. If so, it would suggest that the availability of nesting places does not regulate population density and it could be assumed that a patchy distribution of nesting options does not create these aggregations.

The foraging decisions are relatively simple in the first proposed version of the model. The foraging algorithm is a computational construct that must be calibrated in the final model. However, so far, we have assumed that bees forage for pollen and nectar at the same sites and that they are not constrained by nectar availability (i.e. there is always enough nectar to meet their energy needs). We recognise that this is an oversimplification as not all plants provide pollen and nectar; therefore, bees may have to make additional flights to collect nectar. This may increase foraging time, affect provisioning efficiency and increase the time required for nest construction, especially when floral resources are scarce. Unfortunately, there is a lack of data estimating food intake in *Osmia* spp. (Sgolastra et al. 2019). It is planned to implement a separate study on nectar foraging behaviour in the future model version once the necessary data for parameterisation are available.

The foraging algorithm does not include pollen quality in its decision-making (except for a binary assessment). The degree of specialisation of the host plant amongst bees varies widely and *O. bicornis* is known to be a polylectic/polylege bee. Still, it also shows some preference towards trees, such as *Quercus* spp., *Salix* spp. and *Rosaceae* or herbaceous plants, such as *Ranunculus* spp. (e.g. Persson et al. 2018, Bertrand et al. 2019, Bednarska et al. 2022). There is evidence that *O. bicornis* prefers some types of pollen over others, even if its collection would require flying over long distances and, thus, using more energy resources (own data from the palynological study of pollen provisions and landscape structure show that the bees were collecting pollen from oak trees located ~ 1000 m from the nest instead of pollen from an oilseed rape field located next to the nest; Bednarska et al. 2022). Neither pollen shape nor size explains this opportunistic behaviour (Splitt et al. 2021).

Experimental studies show that the availability of chemical elements in larval food shapes bee fitness. Suboptimal concentrations of certain nutrients in pollen produced by specific plant species reduce bee fitness (Filipiak and Filipiak 2020, Filipiak et al. 2022). This may explain pollen preference in *O. bicornis* towards collecting pollen from various plants to obtain a mixture that provides the right proportion of different elements (nutrients, vitamins

etc.) for optimal offspring development. Therefore, we know that variation in pollen quality is important in the foraging choices of *O. bicornis*. Still, we intend to include this feature in a future version when it is clear whether we have a sufficiently robust pollen quality model to drive *O. bicornis* decisions. This model will have to evaluate different strategies, balancing quality, quantity and distance from the nest.

In the first version of the model, we will not consider nectar as part of the larval diet. This is because only a few studies refer to the pollen/nectar ratio in *Osmia* spp. provisions and, of these, those on *O. bicornis* report a very low proportion of nectar (2-4%; Maddocks and Paulus 1987, Strohm et al. 2002). As studies on other species in the *Osmia* genus suggest higher proportions of nectar in larval provisions (e.g. Sgolastra et al. (2019) reported a pollen/nectar ratio of up to 3:1 for *O. cornuta*), this should be an area for future study. If nectar is an integral part of the provisions of *O. bicornis*, it should be included in future versions of the foraging algorithm.

A new, but significant module to be added to the next version of the model will be the response to pesticides. This model will build on the mechanisms used for honey bees in the ALMaSS (Duan et al. 2022) and be adapted for *O. bicornis* to account for differences in life history and exposure profile.

State variables and scales

See summary of state variables planned to be implemented in the ALMaSS *O. bicornis* model in Table 6.

Table 6.

Summary of state variables planned to be implemented in the ALMaSS *O. bicornis* model. Parameters with the type 'Assumed' are estimated.

Parameter name (including symbol)	Value	Units	Parameter type	Source
Development in the nest				
Lower development threshold (LDT)	Table 3	°C	Estimated from literature	Giejdasz and Wilkaniec (2002), Radmacher and Strohm (2011), Giejdasz et al. (2016)
Sum of effective temperatures (SET)	Table 3	degree days		
Maximum developmental speed for prepupa (*OsmiaPrepupaDevelTotalDays*)	24.3	days		
Variation around maximum developmental speed for prepupa	+/- 10	%	Assumed	-
Overwintering				
Start of pre-wintering	1 September	-	Assumed	-
End of pre-wintering/onset of overwintering	Time threshold *D*; Equation 1 & 2	-	Modelled	-

Parameter name (including symbol)	Value	Units	Parameter type	Source
Temperature threshold for end of pre-wintering/ onset of overwintering (*OsmiaInCocoonPrewinteringTemp Threshold*)	15	°C	Estimated from literature	Sgolastra et al. (2011)
Baseline temperature to calculate sum of effective temperatures during overwintering (*OsmiaInCocoonOverwinteringTempThreshold*)	0	°C	Assumed	-
End of overwintering	1 March	-	Assumed	-
Emergence from the nest				
Emergence counter (*noDaysToEmerge*)	Equation 4	-	Estimated from literature	Fründ et al. (2013)
Temperature threshold for emergence counter (*noDaysToEmerge*)	12	°C		
Emergence distribution	Discrete; Figure 6	-	Estimated based on data from laboratory experiment	A. Bednarska (personal communication)
Osmia mass				
Minimum possible male *mass* (*OsmiaMaleMass Min*)	6.5	mg	Assumed	-
Minimum possible female *mass* (*OsmiaFemaleMassMin*)	50	mg	Assumed	-
Maximum possible female *mass* (*OsmiaFemaleMassMax*)	200	mg	Assumed	-
Size class step for female *mass* (*OsmiaAdultMassCategoryStep*)	10	mg	Assumed	-
Female adult *mass* (*femaleAdultMass*)	Equation 8	-	Estimated from literature	Seidelmann (2006), Seidelmann et al. (2010)
Foraging and dispersal				
Flying weather mean daily wind threshold	8	m/s	Estimated from literature	Bąk et al. (2003)
Flying weather rain daily threshold	0.1	mm		
Flying weather mean daily temperature threshold	13	°C		
Intertegular span (*IT_span*)	Equations 13 and 14	mm	Estimated from literature	Greenleaf et al. (2007)
Typical homing distance (*OsmiaFemaleR50distance*)	Equation 12	m		
Maximum homing distance (*OsmiaFemaleR90distance*)	Equation 11	m		
General movement distribution	Beta; $\alpha = 10$; $\beta = 5$	-	Assumed	-
Nesting				
Duration of pre-nesting (*OsmiaFemalePrenestingDuration*)	2	days	Assumed	-

Parameter name (including symbol)	Value	Units	Parameter type	Source
Minimum number of eggs planned for a nest (*OsmiaMinNoEggsInNest*)	4	-	Assumed	-
Maximum number of eggs planned for a nest (*OsmiaMaxNoEggsInNest*)	25	-	Assumed	-
Distribution for the planned number of eggs in the first nest	Beta; $\alpha = 1.8$; $\beta = 5$	-	Assumed	-
Decrease step for number of eggs in consecutive nests (*DecreaseStepNestSize*)	2	-	Estimated from literature	Giejdasz et al. (2016)
Maximum number of nests possible for a bee (*TotalNestsPossible*)	5	-	Assumed	-
Maximum number of eggs possible for a bee (*TotalEggsPossible*)	Equation 16	-	Assumed	-
Reproduction				
Maximum total number of eggs per bee	Equations 15 and 16	-	Estimated from literature	Seidelmann et al. (2010)
Sex ratio for a given nest	Equation 19	-	Estimated from literature	Ivanov (2006), Seidelmann (2006), Seidelmann et al. (2010)
Provisioning				
Minimum time to construct a cell in days (*tmin*)	1	days	Assumed	-
Maximum time allowed to construct a cell in days (*tmax*)	4	days	Assumed	-
Multiplier to re-calculate from cocooned adult *mass* (*femaleCocoonedMass* / *maleCocoonedMass*) to provision *mass* (*provisionMass*)	3.247	-	Estimated from literature	Seidelmann (2006)
Minimum amount of pollen needed to provision a male cell (*MaleMinTargetProvissionMass*)	10	mg	Estimated based on data from laboratory experiment	A. Bednarska (personal communication)
Maximum difference in cocoon masses produced by a bee in its lifetime (*OsmiaLifetimeCocoonMassLoss*)	30 (+/- 5)	mg	Estimated from literature	Ivanov (2006)
Planned female cocoon *mass* for the first cell in the nest (*firstFemaleCocoonedMass*)	Equation 23	mg	Estimated from literature	Seidelmann (2006), Seidelmann et al. (2010)
Difference between maximum and minimum female cocoon *mass* in a nest (*OsmiaNestCocoonMassLoss*)	15 (+/- 5)	mg	Estimated from literature	Ivanov (2006)
Planned female cocoon *mass* for the next cells in the nest (*femaleCocoonedMass*)	Equation 22	mg	Assumed	-
Mortality				

Parameter name (including symbol)	Value	Units	Parameter type	Source
Daily unspecified mortality for eggs	0.0014	-	Estimated from literature	Radmacher and Strohm (2011)
Daily unspecified mortality for larvae				
Daily unspecified mortality for pre-pupae	0.003	-	Estimated from literature	Radmacher and Strohm (2011), Giejdasz and Fliszkiewicz (2016)
Daily unspecified mortality for pupae				
Overwintering mortality	Equation 23	-	Estimated from literature	Sgolastra et al. (2011)
Daily background mortality rate for females (*OsmiaFemaleBckMort*)	0.02	-	Assumed	-
Maximum lifespan (*OsmiaFemaleLifespan*)	60	days	Assumed	-
Parasitism				
Probability of open cell parasitism	Equation 24	-	Estimated from literature	Seidelmann (2006)
Probability of being parasitised by bombylid fly (*OsmiaBombylidProb)*	0.5	-	Assumed	-
Use of resources				
Minimum nesting density per landscape element type	Table 5	-	Estimated from literature	Koh et al. (2016)
Maximum nesting density per landscape element type				
Decrease in available pollen before a new pollen patch search is initiated (*OsmiaPollenGiveUpThreshold*)	75	%	Assumed	-
Proportion of pollen available to *O. bicornis* individuals (*OsmiaDensityDependentPollenRemovalConst*)	1	-	Assumed	-

Acknowledgements

Funding program

Author contributions

Elżbieta Ziółkowska: Conceptualisation, Methodology, Investigation, Data Curation, Validation, Formal analysis, Visualisation, Writing - Original Draft, Writing - Review & Editing

Christopher J. Topping: Conceptualisation, Methodology, Investigation, Formal analysis, Writing - Review & Editing

Agnieszka J. Bednarska: Conceptualisation, Methodology, Writing- Reviewing and Editing

Ryszard Laskowski: Conceptualisation, Writing - Review & Editing, Project leadership, Funding acquisition

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Disclaimer: This article is (co-)authored by any of the Editors-in-Chief, Managing Editors or their deputies in this journal.

References

- Bąk B, Wilde J, Bratkowski J (2003) The monitoring of the flight activity of the red mason bee (*Osmia rufa* L.). Acta Biologica Universitatis Daugavpiliensis 3 (2): 97-100.
- Bednarska A, Mikołajczyk Ł, Ziółkowska E, Kocjan K, Wnęk A, Mokkapati JS, Teper D, Kaczyński P, Łozowicka B, Śliwińska R, Laskowski R (2022) Effects of agricultural landscape structure, insecticide residues, and pollen diversity on the life-history traits of the red mason bee Osmia bicornis. Science of The Total Environment 809: 151142. https://doi.org/10.1016/j.scitotenv.2021.151142
- Bertrand C, Eckerter P, Ammann L, Entling M, Gobet E, Herzog F, Mestre L, Tinner W, Albrecht M (2019) Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. Journal of Applied Ecology 56 (11): 2431-2442. https://doi.org/10.1111/1365-2664.13483
- Biliński M, Teper D (2004) Rearing and utilization of the red mason bee - *Osmia rufa* L. (Hymenoptera, Megachilidae) for orchard pollination. Journal of Apicultural Science 48: 69-74.
- Bosch J, Blas M (1994) Effect of over-wintering and incubation temperatures on adult emergence in Osmia cornuta Latr (Hymenoptera, Megachilidae). Apidologie 25 (3): 265-277. https://doi.org/10.1051/apido:19940301
- Bosch J, Kemp WP (2000) Development and Emergence of the Orchard Pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). Environmental Entomology 29 (1): 8-13. https://doi.org/10.1603/0046-225x-29.1.8
- Bosch J, Kemp PK (2003) Effect of Wintering Duration and Temperature on Survival and Emergence Time in Males of the Orchard Pollinator *Osmia lignaria* (Hymenoptera:

Megachilidae). Environmental Entomology 32 (4): 711-716. https://doi.org/10.1603/0046-225X-32.4.711

- Bosch J, Kemp W (2004) Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). Apidologie 35 (5): 469-479. https://doi.org/10.1051/apido:2004035

- Bosch J, Vicens N (2006) Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta*. Behavioral Ecology and Sociobiology 60: 26-33. https://doi.org/10.1007/s00265-005-0134-4

- Bosch J, Sgolastra F, Kemp WP (2008) Life Cycle Ecophysiology of Osmia Mason Bees Used as Crop Pollinators. In: James RR, Pitts-Singer TL (Eds) Bee Pollination in Agricultural Ecosystems. Oxford University Press, New York, 232 pp. https://doi.org/10.1093/acprof:oso/9780195316957.001.0001

- Bosch J, Sgolastra F, Kemp W (2010) Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. Journal of Insect Physiology 56 (12): 1949-1957. https://doi.org/10.1016/j.jinsphys.2010.08.017

- Brittain C, Potts S (2011) The potential impacts of insecticides on the life-history traits of bees and the consequences for pollination. Basic and Applied Ecology 12 (4): 321-331. https://doi.org/10.1016/j.baae.2010.12.004

- Bukovinszky T, Rikken I, Evers S, Wäckers F, Biesmeijer J, Prins HT, Kleijn D (2017) Effects of pollen species composition on the foraging behaviour and offspring performance of the mason bee *Osmia bicornis* (L.). Basic and Applied Ecology 18: 21-30. https://doi.org/10.1016/j.baae.2016.11.001

- Coudrain V, Rittiner S, Herzog F, Tinner W, Entling M (2016) Landscape distribution of food and nesting sites affect larval diet and nest size, but not abundance of *Osmia bicornis*. Insect Science 23 (5): 746-753. https://doi.org/10.1111/1744-7917.12238

- Duan X, Wallis D, Hatjina F, Simon-Delso N, Bruun Jensen A, Topping CJ (2022) ApisRAM Formal Model Description. EFSA Supporting Publications 19 (2). https://doi.org/10.2903/sp.efsa.2022.en-7184

- EFSA (2013) Guidance on the risk assessment of plant protection products on bees (*Apis mellifera*, *Bombus* spp. and solitary bees). EFSA Journal 11 (7). https://doi.org/10.2903/j.efsa.2013.3295

- Everaars J, Strohbach M, Gruber B, Dormann C (2011) Microsite conditions dominate habitat selection of the red mason bee (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. Landscape and Urban Planning 103 (1): 15-23. https://doi.org/10.1016/j.landurbplan.2011.05.008

- Everaars J, Dormann C (2014) Simulation of Solitary (Non-Apis) Bees Competing for Pollen. In: Devillers J (Ed.) In Silico Bees. CRC Press, Boca Raton, 314 pp. https://doi.org/10.1201/b16453

- Felicioli A, Ambroselli S, Cilia G, Sagona S (2017) Parasitization of a wild and reared population of the solitary bee *Osmia cornuta* Latr. by the parasitoid *Anthrax anthrax* Schrank (Diptera, Bombyliidae): comparison between two types of artificial nest. Journal of Apicultural Research 56 (5): 598-605. https://doi.org/10.1080/00218839.2017.1343019

- Felicioli A, Sagona S, Galloni M, Bortolotti L, Bogo G, Guarnieri M, Nepi M (2018) Effects of nonprotein amino acids on survival and locomotion of *Osmia bicornis*. Insect Molecular Biology 27 (5): 556-563. https://doi.org/10.1111/imb.12496
- Filipiak M (2019) Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. Journal of Applied Ecology 56 (6): 1410-1418. https://doi.org/10.1111/1365-2664.13383
- Filipiak Z, Filipiak M (2020) The Scarcity of Specific Nutrients in Wild Bee Larval Food Negatively Influences Certain Life History Traits. Biology 9 (12). https://doi.org/10.3390/biology9120462
- Filipiak Z, Denisow B, Stawiarz E, Filipiak M (2022) Unravelling the dependence of a wild bee on floral diversity and composition using a feeding experiment. Science of The Total Environment 820 https://doi.org/10.1016/j.scitotenv.2022.153326
- Fliszkiewicz M, Kuśnierczak A, Szymaś B (2012) The Accompanying Fauna of Solitary Bee *Osmia Bicornis* (L.) Syn. *Osmia Rufa* (L.) Nests Settled in Different Biotopes. Journal of Apicultural Science 56 (1). https://doi.org/10.2478/v10289-012-0006-x
- Fründ J, Zieger S, Tscharntke T (2013) Response diversity of wild bees to overwintering temperatures. Oecologia 173 (4): 1639-1648. https://doi.org/10.1007/s00442-013-2729-1
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhoffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipolito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlof M, Seymour CL, Schuepp C, Szentgyorgyi H, Taki H, Tscharntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM (2013) Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339 (6127): 1608-1611. https://doi.org/10.1126/science.1230200
- Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71 (5): 757-764. https://doi.org/10.1046/j.1365-2656.2002.00641.x
- Giejdasz K, Wilkaniec Z (2002) Individual development of the red mason bee (*Osmia rufa* L., Megachilidae) under natural and laboratory conditions. Journal of Apicultural Science 46: 51-57.
- Giejdasz K, Fliszkiewicz M (2016) Effect of temperature treatment during development of *Osmia rufa* L., on mortality, emergence and longevity of adults. Journal of Apicultural Science 60 (2): 221-232. https://doi.org/10.1515/jas-2016-0029
- Giejdasz K, Fliszkiewicz M, Bednárová A, Krishnan N (2016) Reproductive potential and nesting effects of *Osmia rufa* (syn. *bicornis*) female (Hymenoptera: Megachilidae). Journal of Apicultural Science 60 (1): 75-86. https://doi.org/10.1515/jas-2016-0003
- Giejdasz K, Wasielewski O (2017) Effect of Artificial Prolonged Wintering on Emergence and Survival of *Osmia Rufa* Adults. Journal of Apicultural Science 61 (1): 127-137. https://doi.org/10.1515/jas-2017-0011
- Goodell K (2003) Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. Oecologia 134 (4): 518-527. https://doi.org/10.1007/s00442-002-1159-2

- Goulson D, Nicholls E, Botías C, Rotheray E (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347 (6229). https://doi.org/10.1126/science.1255957
- Greenleaf S, Williams N, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153 (3): 589-596. https://doi.org/10.1007/s00442-007-0752-9
- Grimm V, Railsback S (2005) Individual-based Modeling and Ecology. Princeton University Press, 448 pp. URL: http://www.jstor.org/stable/j.ctt5hhnk8
- Groulx A, Forrest JK (2018) Nesting aggregation as a predictor of brood parasitism in mason bees (*Osmia* spp.). Ecological Entomology 43 (2): 182-191. https://doi.org/10.1111/een.12484
- Gruber B, Eckel K, Everaars J, Dormann C (2011) On managing the red mason bee (*Osmia bicornis*) in apple orchards. Apidologie 42 (5). https://doi.org/10.1007/s13592-011-0059-z
- Guédot C, Bosch J, Kemp W (2009) Relationship between body size and homing ability in the genus *Osmia* (Hymenoptera; Megachilidae). Ecological Entomology 34 (1): 158-161. https://doi.org/10.1111/j.1365-2311.2008.01054.x
- Haider M, Dorn S, Sedivy C, Müller A (2014) Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini). Biological Journal of the Linnean Society 111 (1): 78-91. https://doi.org/10.1111/bij.12186
- Hersbach H, Bell B, Berrisford P, Biavati G, Horányi A, Muñoz Sabater J, Nicolas J, Peubey C, Radu R, Rozum I, Schepers D, Simmons A, Soci C, Dee D, Thépaut J (2023) ERA5 hourly data on single levels from 1940 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). URL: 10.24381/cds.adbb2d47
- Ivanov SP (2006) The nesting of *Osmia rufa* (L.) (Hymenoptera, Megachilidae) in the Crimea: Structure and composition of nests. Entomological Review 86 (5): 524-533. https://doi.org/10.1134/s0013873806050046
- Kemp WP, Bosch J (2005) Effect of Temperature on *Osmia lignaria* (Hymenoptera: Megachilidae) Prepupa–Adult Development, Survival, and Emergence. Journal of Economic Entomology 98 (6): 1917-1923. https://doi.org/10.1093/jee/98.6.1917
- Koh I, Lonsdorf E, Williams N, Brittain C, Isaacs R, Gibbs J, Ricketts T (2016) Modeling the status, trends, and impacts of wild bee abundance in the United States. Proceedings of the National Academy of Sciences 113 (1): 140-145. https://doi.org/10.1073/pnas.1517685113
- Kratschmer S, Petrović B, Curto M, Meimberg H, Pachinger B (2020) Pollen availability for the Horned mason bee (*Osmia cornuta*) in regions of different land use and landscape structures. Ecological Entomology 45 (3): 525-537. https://doi.org/10.1111/een.12823
- Krunić M, Stanisavljević L, Pinzauti M, Felicioli A (2005) The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. Bulletin of Insectology 58: 141-152.
- Maddocks R, Paulus HF (1987) Quantitative Aspekte der Brutbiologie von *Osmia rufa* L. und *Osmia cornuta* Latr. (Hymenoptera, Megachilidae): Eine vergleichende Untersuchung zu Mechanismen der Konkurrenzminderung zweier nahverwandter Bienenarten. Zoologische Jahrbücher Abteilung für Systematik, Geographie und Biologie der Tiere 114: 15-44.

- McKinney M, Ahn JJ, Park Y (2017) Thermal biology of *Osmia cornifrons* (Hymenoptera: Megachilidae) eggs and larvae. Journal of Apicultural Research 56 (4): 421-429. https://doi.org/10.1080/00218839.2017.1327935
- Mokkapati JS, Bednarska A, Laskowski R (2021) The development of the solitary bee *Osmia bicornis* is affected by some insecticide agrochemicals at environmentally relevant concentrations. Science of The Total Environment 775 https://doi.org/10.1016/j.scitotenv.2021.145588
- More S, Bampidis V, Benford D, Bragard C, Halldorsson T, Hernández-Jerez A, Bennekou SH, Koutsoumanis K, Machera K, Naegeli H, Nielsen SS, Schlatter J, Schrenk D, Silano V, Turck D, Younes M, Arnold G, Dorne J, Maggiore A, Pagani S, Szentes C, Terry S, Tosi S, Vrbos D, Zamariola G, Rortais A (2021) A systems-based approach to the environmental risk assessment of multiple stressors in honey bees. EFSA Journal 19 (5). https://doi.org/10.2903/j.efsa.2021.6607
- Nilsson S, Franzén M, Pettersson L (2013) Land-use changes, farm management and the decline of butterflies associated with semi-natural grasslands in southern Sweden. Nature Conservation 6: 31-48. https://doi.org/10.3897/natureconservation.6.5205
- Persson A, Mazier F, Smith H (2018) When beggars are choosers-How nesting of a solitary bee is affected by temporal dynamics of pollen plants in the landscape. Ecology and Evolution 8 (11): 5777-5791. https://doi.org/10.1002/ece3.4116
- Potts S, Biesmeijer J, Kremen C, Neumann P, Schweiger O, Kunin W (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25 (6): 345-353. https://doi.org/10.1016/j.tree.2010.01.007
- Potts SG, Roberts SPM, Dean R, Marris G, Brown MA, Jones R, Neumann P, Settele J (2010) Declines of managed honey bees and beekeepers in Europe. Journal of Apicultural Research 49 (1): 15-22. https://doi.org/10.3896/ibra.1.49.1.02
- Powney G, Carvell C, Edwards M, Morris RA, Roy H, Woodcock B, Isaac NB (2019) Widespread losses of pollinating insects in Britain. Nature Communications 10 (1). https://doi.org/10.1038/s41467-019-08974-9
- Radmacher S, Strohm E (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). Apidologie 41 (2): 169-177. https://doi.org/10.1051/apido/2009064
- Radmacher S, Strohm E (2011) Effects of constant and fluctuating temperatures on the development of the solitary bee *Osmia bicornis* (Hymenoptera: Megachilidae). Apidologie 42 (6): 711-720. https://doi.org/10.1007/s13592-011-0078-9
- Raw A (1972) The biology of the solitary bee *Osmia rufa* (L.) (Megachilidae). Transactions of the Royal Entomological Society of London 124: 213-229. https://doi.org/10.1111/j.1365-2311.1972.tb00364.x
- Raw A (1974) Pollen Preferences of Three Osmia Species (Hymenoptera). Oikos 25 (1): 54-60. https://doi.org/10.2307/3543545
- Sánchez-Bayo F, Wyckhuys KG (2019) Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232: 8-27. https://doi.org/10.1016/j.biocon.2019.01.020
- Sedivy C, Müller A, Dorn S (2011) Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: evidence for physiological adaptations to digest pollen. Functional Ecology 25 (3): 718-725. https://doi.org/10.1111/j.1365-2435.2010.01828.x

- Sedivy C, Dorn S (2014) Towards a sustainable management of bees of the subgenus Osmia (Megachilidae; Osmia) as fruit tree pollinators. Apidologie 45 (1): 88-105. https://doi.org/10.1007/s13592-013-0231-8
- Seibold S, Gossner M, Simons N, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bauhus J, Fischer M, Habel J, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze E, Vogt J, Wöllauer S, Weisser W (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574 (7780): 671-674. https://doi.org/10.1038/s41586-019-1684-3
- Seidelmann K (2006) Open-cell parasitism shapes maternal investment patterns in the Red Mason bee *Osmia rufa*. Behavioral Ecology 17 (5): 839-848. https://doi.org/10.1093/beheco/arl017
- Seidelmann K, Ulbrich K, Mielenz N (2010) Conditional sex allocation in the Red Mason bee, *Osmia rufa*. Behavioral Ecology and Sociobiology 64 (3): 337-347. https://doi.org/10.1007/s00265-009-0850-2
- Seidelmann K, Bienasch A, Pröhl F (2016) The impact of nest tube dimensions on reproduction parameters in a cavity nesting solitary bee, *Osmia bicornis* (Hymenoptera: Megachilidae). Apidologie 47 (1): 114-122. https://doi.org/10.1007/s13592-015-0380-z
- Seidelmann K (2018) Optimal resource allocation, maternal investment, and body size in a solitary bee, *Osmia bicornis*. Entomologia Experimentalis et Applicata 166 (9): 790-799. https://doi.org/10.1111/eea.12711
- Sgolastra F, Kemp W, Buckner J, Pitts-Singer T, Maini S, Bosch J (2011) The long summer: Pre-wintering temperatures affect metabolic expenditure and winter survival in a solitary bee. Journal of Insect Physiology 57 (12): 1651-1659. https://doi.org/10.1016/j.jinsphys.2011.08.017
- Sgolastra F, Kemp W, Maini S, Bosch J (2012) Duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures in bees of the genus Osmia. Journal of Insect Physiology 58 (7): 924-933. https://doi.org/10.1016/j.jinsphys.2012.04.008
- Sgolastra F, Arnan X, Pitts-Singer T, Maini S, Kemp W, Bosch J (2016) Pre-wintering conditions and post-winter performance in a solitary bee: does diapause impose an energetic cost on reproductive success? Ecological Entomology 41 (2): 201-210. https://doi.org/10.1111/een.12292
- Sgolastra F, Hinarejos S, Pitts-Singer TL, Boyle NK, Joseph T, Luckmann J, Raine NE, Singh R, Williams NM, Bosch J (2019) Pesticide Exposure Assessment Paradigm for Solitary Bees. Environmental entomology 48 (1): 22-35. https://doi.org/10.1093/ee/nvy105
- Sharpe PH, DeMichele D (1977) Reaction kinetics of poikilotherm development. Journal of Theoretical Biology 64 (4): 649-670. https://doi.org/10.1016/0022-5193(77)90265-x
- Smith C, Fretwell S (1974) The Optimal Balance between Size and Number of Offspring. The American Naturalist 108 (962): 499-506. https://doi.org/10.1086/282929
- Söderman AE, Irminger Street T, Hall K, Olsson O, Prentice H, Smith H (2018) The value of small arable habitats in the agricultural landscape: Importance for vascular plants and the provisioning of floral resources for bees. Ecological Indicators 84: 553-563. https://doi.org/10.1016/j.ecolind.2017.09.024
- Splitt A, Skórka P, Strachecka A, Borański M, Teper D (2021) Keep trees for bees: Pollen collection by *Osmia bicornis* along the urbanization gradient. Urban Forestry & Urban Greening 64 https://doi.org/10.1016/j.ufug.2021.127250

- Steffan-Dewenter I, Schiele S (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats? Ecology 89 (5): 1375-1387. https://doi.org/10.1890/06-1323.1
- Strohm E, Daniels H, Warmers C, Stoll C (2002) Nest provisioning and a possible cost of reproduction in the megachilid bee *Osmia rufa* studied by a new observation method. Ethology Ecology & Evolution 14 (3): 255-268. https://doi.org/10.1080/08927014.2002.9522744
- Szentgyörgyi H, Woyciechowski M (2013) Cocoon orientation in the nests of red mason bees (*Osmia bicornis*) is affected by cocoon size and available space. Apidologie 44 (3): 334-341. https://doi.org/10.1007/s13592-012-0185-2
- Szentgyörgyi H, Moroń D, Nawrocka A, Tofilski A, Woyciechowski M (2017) Forewing structure of the solitary bee *Osmia bicornis* developing on heavy metal pollution gradient. Ecotoxicology 26 (8): 1031-1040. https://doi.org/10.1007/s10646-017-1831-2
- Teper D, Biliński M (2009) Red mason bee (*Osmia rufa* L.) as a pollinator of rape plantations. Journal of Apicultural Science 53: 115-120.
- Topping C, Hansen T, Jensen T, Jepsen J, Nikolajsen F, Odderskær P (2003) ALMaSS, an agent-based model for animals in temperate European landscapes. Ecological Modelling 167: 65-82. https://doi.org/10.1016/s0304-3800(03)00173-x
- Topping C, Craig P, de Jong F, Klein M, Laskowski R, Manachini B, Pieper S, Smith R, Sousa JP, Streissl F, Swarowsky K, Tiktak A, van der Linden T (2015) Towards a landscape scale management of pesticides: ERA using changes in modelled occupancy and abundance to assess long-term population impacts of pesticides. Science of The Total Environment 537: 159-169. https://doi.org/10.1016/j.scitotenv.2015.07.152
- Topping C, Dalby L, Skov F (2016) Landscape structure and management alter the outcome of a pesticide ERA: Evaluating impacts of endocrine disruption using the ALMaSS European Brown Hare model. Science of The Total Environment 541: 1477-1488. https://doi.org/10.1016/j.scitotenv.2015.10.042
- Topping CJ, Brown M, Chetcuti J, de Miranda J, Nazzi F, Neumann P, Paxton R, Rundlöf M, Stout J (2021) Holistic environmental risk assessment for bees. Science 371 (6532): 897-897. https://doi.org/10.1126/science.abg9622
- Topping CJ (2022) The Animal Landscape and Man Simulation System (ALMaSS): a history, design, and philosophy. Research Ideas and Outcomes 8 https://doi.org/10.3897/rio.8.e89919
- Topping CJ, Kondrup Marcussen L, Thomsen P, Chetcuti J (2022) The Formal Model article format: justifying modelling intent and a critical review of data foundations through publication. Food and Ecological Systems Modelling Journal 3 https://doi.org/10.3897/fmj.3.91024
- Torchio PF (1984) Field Experiments with the Pollinator Species, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae) in Apple Orchards: III, 1977 Studies. Journal of the Kansas Entomological Society 57 (3): 517-521.
- Uhl P, Brühl C (2019) The Impact of Pesticides on Flower-Visiting Insects: A Review with Regard to European Risk Assessment. Environmental Toxicology and Chemistry 38 (11): 2355-2370. https://doi.org/10.1002/etc.4572
- Ulbrich K, Seidelmann K (2001) Modeling population dynamics of solitary bees in relation to habitat quality. Web Ecology 2 (1): 57-64. https://doi.org/10.5194/we-2-57-2001

- Urbanowicz C, Muñiz P, McArt S (2020) Honey bees and wild pollinators differ in their preference for and use of introduced floral resources. Ecology and Evolution 10 (13): 6741-6751. https://doi.org/10.1002/ece3.6417
- Willmer PG, Cunnold H, Ballantyne G (2017) Insights from measuring pollen deposition: quantifying the pre-eminence of bees as flower visitors and effective pollinators. Arthropod-Plant Interactions 11 (3): 411-425. https://doi.org/10.1007/s11829-017-9528-2
- Winfree R, Williams N, Gaines H, Ascher J, Kremen C (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. Journal of Applied Ecology 45 (3): 793-802. https://doi.org/10.1111/j.1365-2664.2007.01418.x
- Zajdel B, Fliszkiewicz M, Kucharska K, Gąbka J (2016) Influence of the presence of *Cacoxenus indagator* Loew. parasite larvae in brood chambers on the emergence rate and size of red mason bees. Medycyna Weterynaryjna 72 (9): 567-570. https://doi.org/10.21521/mw.5559
- Ziółkowska E, Topping C, Bednarska A, Laskowski R (2021) Supporting non-target arthropods in agroecosystems: Modelling effects of insecticides and landscape structure on carabids in agricultural landscapes. Science of The Total Environment 774 https://doi.org/10.1016/j.scitotenv.2021.145746
- Ziółkowska E, Tiktak A, Topping C (2022) Is the effectiveness of policy-driven mitigation measures on carabid populations driven by landscape and farmland heterogeneity? Applying a modelling approach in the Dutch agroecosystems. PLOS ONE 17 (12). https://doi.org/10.1371/journal.pone.0279639