Nesting, foraging and parasites

By Liam Olds

Life expectancy

- Typical solitary bee lifespan = **few weeks to a month.**
- **Adult activity coincides with floral resource availability**.
- Most solitary bee **species** are **active for months** because they are **multivoltine** (two or more broods of offspring per year) and have **broad host-plant preferences**.
- **Much of lifespan is spent over-wintering as an adult** (many *Osmia, Andrena,* and some *Colletes* and *Megachile*) **or late-instar larva** – except *Colletes halophilus* & *C. collaris* that overwinter as 2nd and 3rd instar larvae for reasons unknown.
- **Low lifetime fecundity** (i.e. produce few offspring) **in most solitary bees** – due to short adult lifespan and low rate of cell provisioning.

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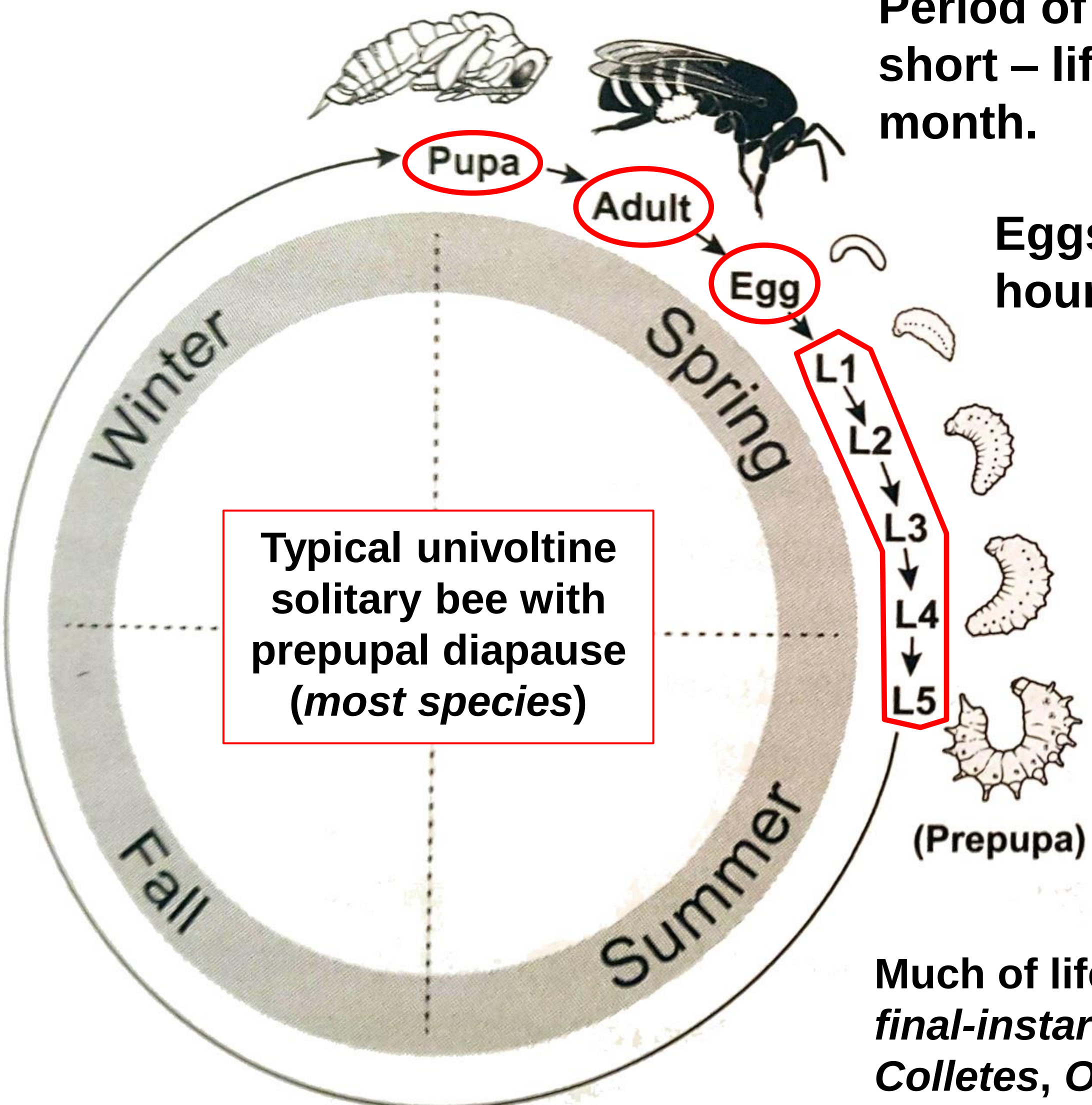
In most species the **pupal stage is short (1-2 weeks) – vulnerable state.**

Period of adult activity is generally short – lifespan from few weeks to a month.



Eggs generally hatch within hours.

Bees go through 5 larval stages (instars).

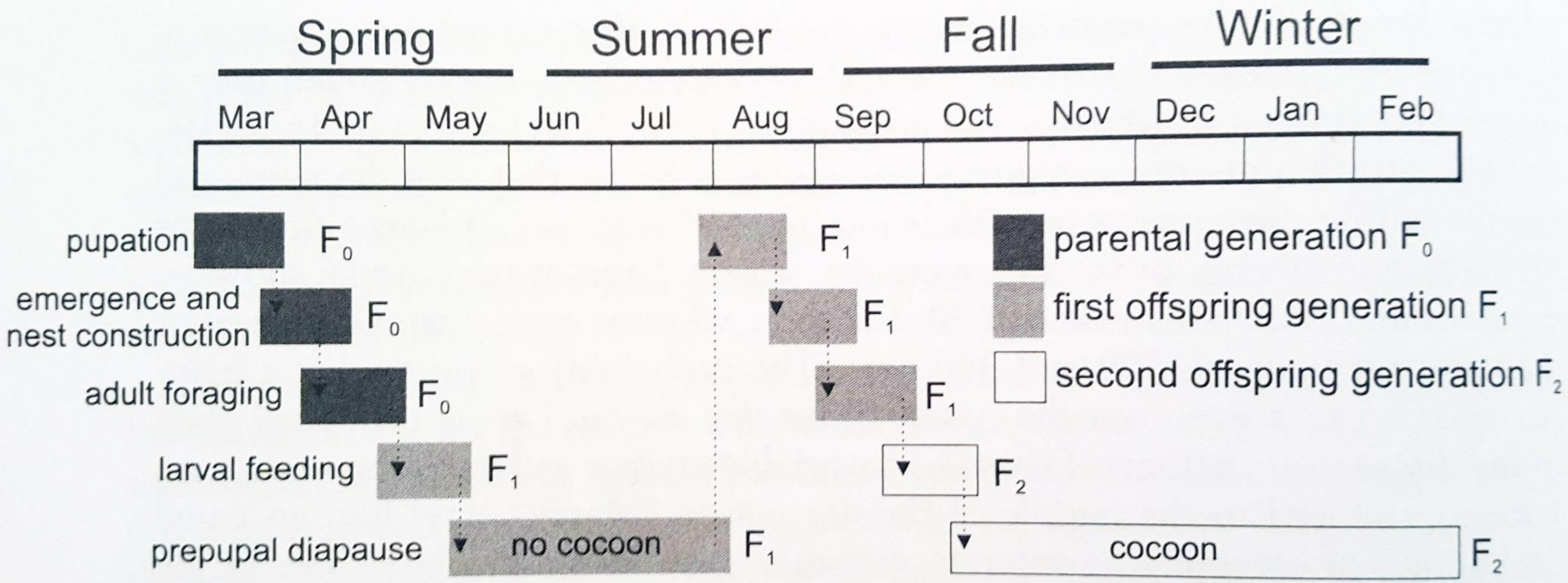
Larval development is usually rapid and most larvae complete feeding between 1-3 weeks.

Much of lifecycle is spent over-wintering as *final-instar larva* (prepupa) or *adult* (e.g. in *Colletes*, *Osmia* and *Megachile*) within the brood cell.

Cocoon

- **Some bees spin a cocoon** before pupating.
- Cocoon **protects prepupa from parasites and desiccation** (drying-out) but is costly to produce.
- In UK bee genera – all Megachilidae (*Anthidium*, *Chelostoma*, *Coelioxys*, *Heriades*, *Hoplitis*, *Megachile*, *Osmia*, *Stelis*) and *Eucera*, *Macropsis*, *Melecta* and *Melitta* spin cocoons.
- **Take a look at *Osmia* cocoons I have brought along!**

Bivoltine with prepupal diapause

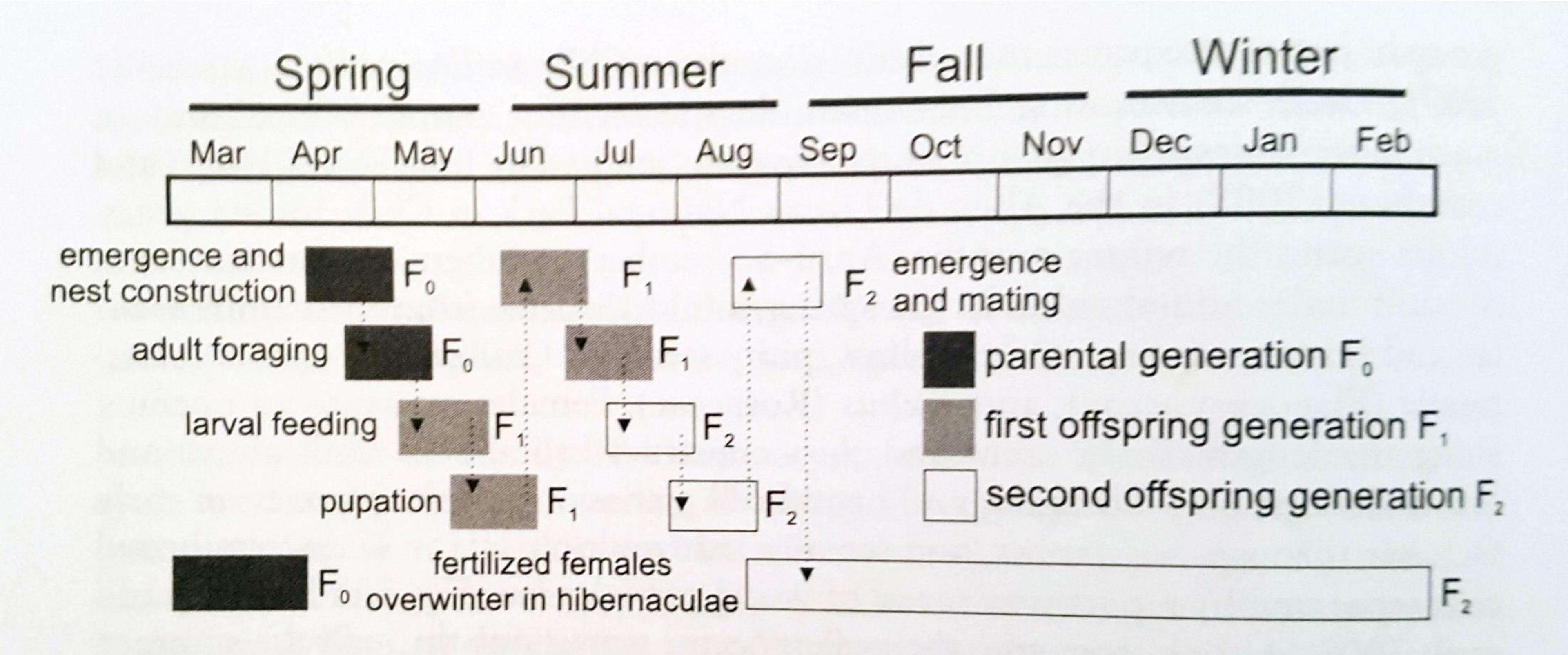


Bivoltine; larval diapause (e.g., *Anthophorula sidae*)

Figure 3-16. Life cycle of a desert, bivoltine bee with prepupal diapause (e.g., *Anthophorula sidae*; Rozen 1984a). F_0 = parental generation, F_1 = first offspring generation, F_2 = second offspring generation.

Andrena flavipes

Bivoltine with overwintering fertilised females



© Danforth, Minckley and Neff (2019)

- **Only fertilised, adult females over-winter.**
- **Mating takes place late in the season** and males die before onset of winter.
- These females **do not construct nests or start provisioning brood cells** but instead over-winter.

Parsivoltinism

- Some species (e.g. *Osmia leaiana*) can exhibit parsivoltinism.
- Such parsivoltine bees require 2 years to complete development.
- Reasons are unknown but cannot be solely explained by environmental factors acting on the female parent or her offspring.
- Nests can contain both one- and two-year forms.
- As such, care needs to be taken when 'cleaning' bee hotels.

Osmia leaiana

Bumblebee lifecycle © BBCT

Nesting – bumblebees

- Bumblebees nest in a variety of locations:
  - abandoned mammal burrows
  - compost heaps
  - under sheds
  - tall grass
  - bird boxes
  - lofts
  - in trees

Nesting – 4 major strategies

1. **Ground-nesting (soil excavators)**
   - Majority of UK species
   - ALL **Andrenidae** and **Melittidae**, MOST **Colletidae** and **Halictidae**, and a large proportion of non-parasitic **Apidae**
   - Flat ground, slopes or vertical faces
   - Ground normally has be **dry and exposed to the sun**
   - Cells are usually lined with **waxy glandular secretions** (cellophane-like substance in *Colletes* and *Hylaeus*), and some use **floral oils** (*Macropsis*).

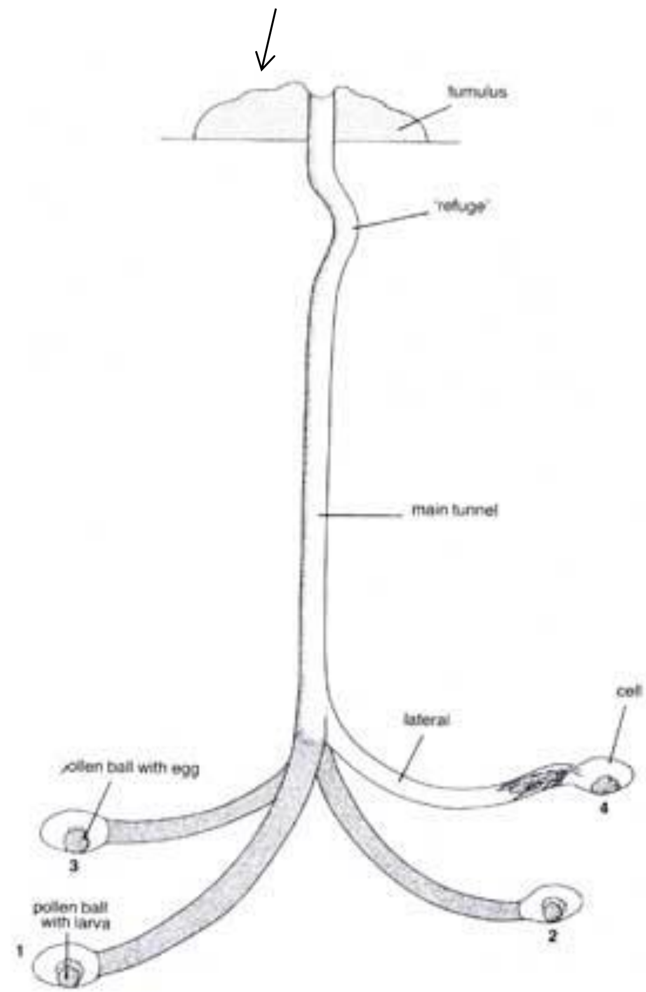
Andrena humilis

Colletes hederae

Ground nesting

Majority of bees simply pile loose soil at nest entrance to form a volcano-like mound (**tumulus**)

- **~64%** of all non-parasitic bee species worldwide are ground-nesting, soil-excavating bees.
- Typical bee nest consists of a **vertical burrow**, with **lateral tunnels** leading to **brood cells.**
- **Maximum depth** for most bee nests **averages 35cm** (13.8”).
- Some build brood cells immediately off the main burrow.
- Brood cells may be arranged **singly, in clusters or in a linear series.**
- Use their mandibles and/or legs used to dig burrow.



Typical *Andrena* mining bee nest from “Bees of the World” by Christopher O’Toole and Anthony Raw

Ground nesting

- Soil texture, ground cover and aspect all determine the locations of nests.
- Most solitary bees have a **preference for nesting where their mother nested** → particularly so in communal species where females reuse their mother's nest over many generations.
- Ground-nesting bee **aggregations can persist for many decades** (as long as 60 years!).
- Ground-nesting bees (especially those that nest in large aggregations) are **capable of moving considerable amounts of soil** → contribute to **soil aeration and rejuvenation.**

2. Renters

generally do well in small, fragmented urban & suburban habitats

- Nest in **pre-existing cavities** including holes in the ground, cavities in stone, gaps in masonry, old beetle burrows, snail shells, and vacated fly galls.
- Exemplified by *Anthidium*, *Megachile* and *Osmia.*
- Arrange nests in a **linear sequence** (males generally nearer entrance).
- Walls and partitions constructed from **leaf sections** (*Megachile*), **mud** (*Osmia bicornis*), **mud mixed with nectar** (*Chelostoma*), **chewed-up leaf mastic** (various *Osmia*), **plant hairs** (*Anthidium*), **plant/tree resin** (*Heriades truncorum*)…

…also sand, pebbles, flower petals and even plastics!


Most cavity nesters (renters) are generalised in their choice of nest site, but **some are highly specialised.**

Three *Osmia* species nest in empty snail shells:

aurulenta, ***bicolor*** and ***spinulosa***

A number of nest cells may fit into one shell.

Osmia bicolor © Phil Clayton

https://www.youtube.com/watch?v=NVINmxCImzI

Osmia bicolor artwork by John Walters

3. **Wood excavators**

- Excavate nests in **solid wood** *(Xylocopa*)*,* **rotten or soft wood** (some *Megachile*), and **pithy stems** (*Ceratina* and *Hoplitis*).
- Mandibular modifications associated with excavating into wood.
- Walls and partitions constructed from **sawdust or wood fragments** (*Xylocopa*), **leaf sections** (*Megachile*), **soil** or **chewed-up leaf mastic** (*Hoplitis*).

4. **Above-ground builders (construct freestanding nests of various materials) – no UK species**

Brood cells

- **ALL non-parasitic bees build brood cells** to house pollen/nectar/ floral oils and serve as home for developing larvae/adult.
- In most bees, the pollen/nectar provisions are either **loosely constructed masses** or **compact loaves or balls**.
- **Most line their brood cells** (glandular secretion, plant material) → barrier to desiccation, flooding, microbes, parasites and predators. **Some don't** (e.g. *Dasypoda*) – adaptation to dry environments?

Osmia bicornis © tpjunier

Foraging

- Interaction between bees and plants = **“balanced mutual exploitation”.**
- **3 primary floral resources** used in brood-cell provisioning:
  - **Nectar** = source of sugar (energy); cheap for plant to produce
  - **Pollen** = source of protein; can contain >60% protein (beef is ~ 26%!)
  - **Floral oils** = highly valuable to bees; costly for plant
- ~**32% of bee species use non-floral resources** (e.g. honeydew and extra-floral nectaries, fragrances for mate attraction, resins for self-medication, plant material for nest construction).
- **Pollen is the most important floral resource** harvested by bees → needed for **larval development** and **egg production.**
- Females must typically harvest **3-4 times their dry body weight in pollen** to provision a single brood cell!

How do solitary bees collect pollen?

- Finely **branched, plumose body hairs**.
- **Diversity of brushes/combs** on fore-, mid- and hind-legs.
- **Pollen brush** (solitary bees) **for transporting pollen back to the nest** (except parasitic species and *Hylaeus*).
- **Galeal or spipital comb** to groom pollen from the fore-legs.
- ALL bees possess an **antennal cleaner** on fore-legs.
- When a bee flies, it builds up **electrostatic charge** which causes pollen to stick to the body hairs.


Pollen brush (scopa) of *Andrena*

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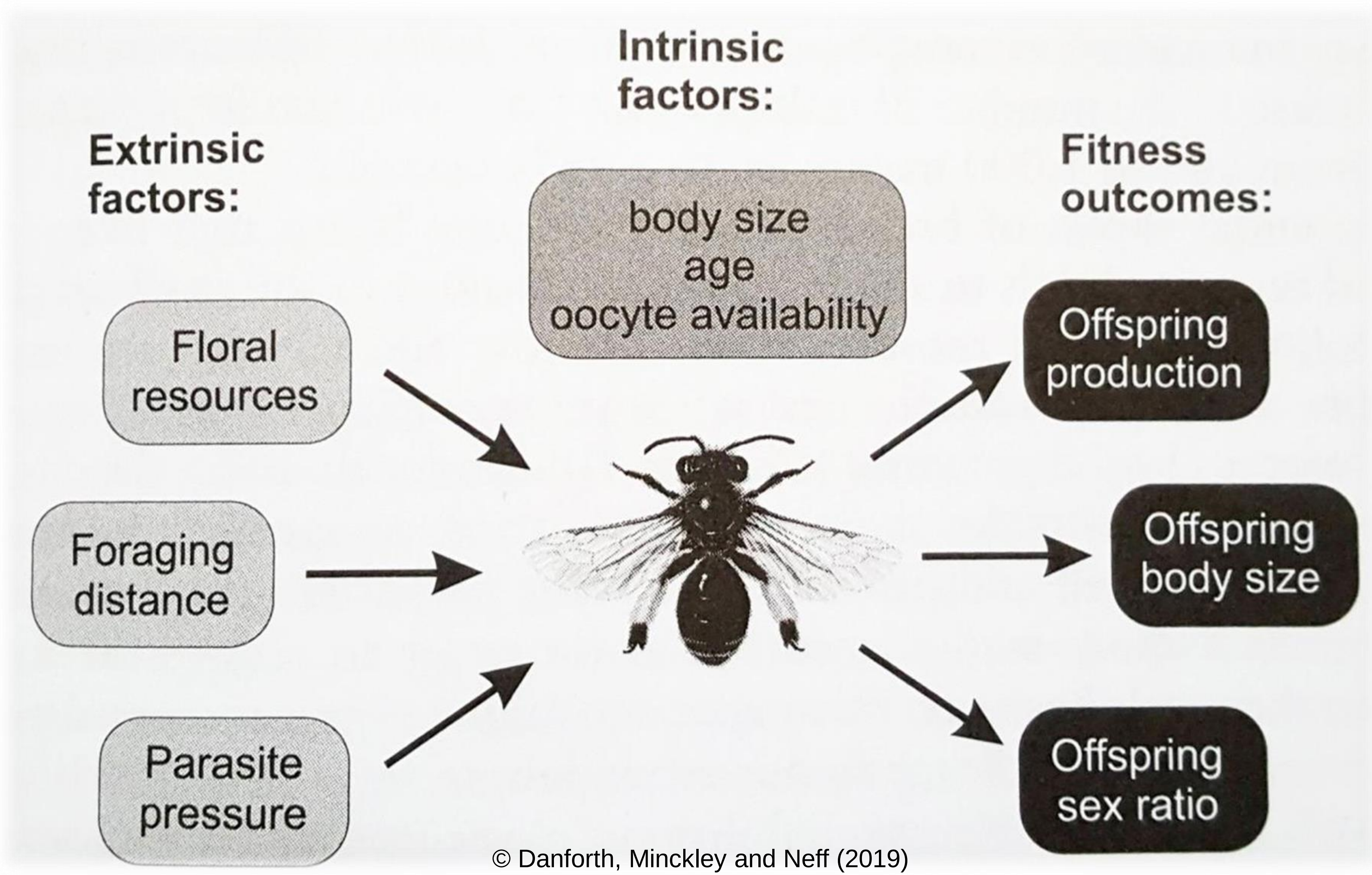
Foraging

Shape and **size** of body, and the **length and structure of the tongue** can dictate which flowers are used.

These categories:

- **Polylectic** (majority of UK bees) → pollen obtained from variety of plant species in numerous genera/families.
- **Oligolectic** → pollen obtained from plants of a single genus or group of closely related genera.
- **Monolectic** → pollen obtained from a single plants species.

Factors affecting foraging & offspring production in solitary bees



Intrinsic factors:

body size
age
oocyte availability

Larger = produce more offspring.

Younger = gather more pollen & make fewer trips.

Often 1 egg per day in solitary bees (1000+ in honeybee queens).

Extrinsic factors:

Floral resources

Activity tracks floral resource availability; greater floral resources = **more brood cells provisioned and greater investment in females.**

Foraging distance

Foraging range for most species is **under 500m** (rare to forage over 1km); +ve correlation between body size & foraging distance.

Parasite pressure

When high = fewer trips & **spend more time in the nest** (guarding); also create more nests with few brood cells for each (spreading out offspring geographically).

Sex determination

- **Females can decide what sex they produce!**
- For females, mother makes a larger brood cell larger and provision it with more pollen (females are generally larger and require more pollen; **females are costly to produce**).
- **Males are cheap to produce** (require smaller brood cell and less provisions).
- **When resources are limited, females may be forced to produce males.**

Friend or foe

- Whole host of organisms interact with adult bees and their larvae including **birds, mammals, spiders, mites, flies, beetles, wasps, true bugs, bacteria, fungi, yeast, nematodes**…

- These can be:

  - **Predators** (eat many prey)
  - **Parasites** (take resources from one host)
  - **Brood parasites** (using nest provisions)
  - **Parasitoids** (like parasites but *always* kill their host)
  - **Pathogenic** (disease causing - e.g. Bacteria)
  - **Mutualistic** (beneficial)
  - **Commensal** (no harm)

Predators

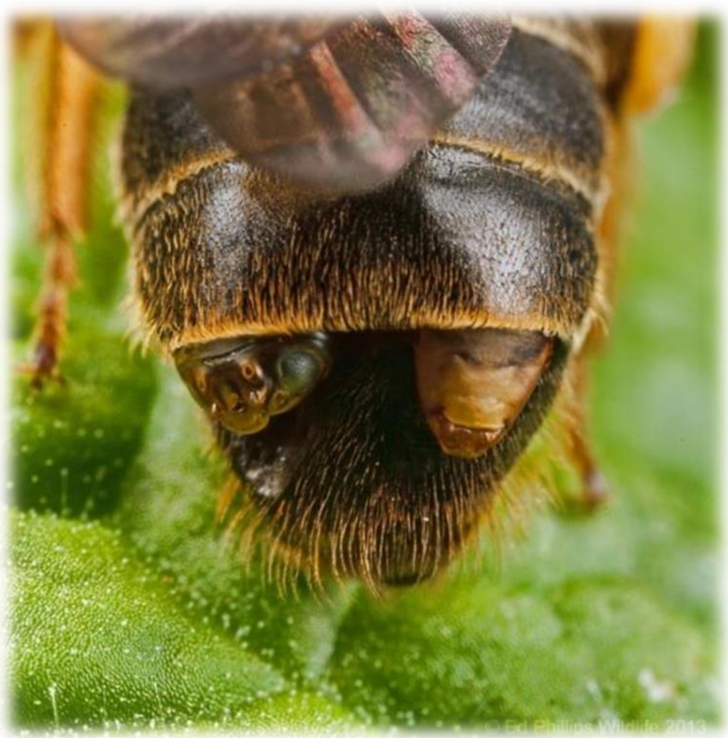
- **Birds (e.g. tits)**, **mammals**, **robber flies**, **crab spiders**, **ants**, **assassin bugs**, **crabronid wasps** and **dragonflies** will all catch and eat adult bees.
- **Mites** and ***Trichodes* beetles** will also predate bee larvae.

Misumena vatia

Cerceris rybyensis

Parasites of solitary bees - Stylopids

- Begin life as mobile triungulin that rest on flowers.



© Ed Phillips

- They get picked up by adult bees while foraging and taken back to the bees nest.
- Once inside the nest, the triungulin seeks out and enters a host egg or larva.
- Once inside the host, they become simple legless forms and remain inside the host body, going through several moults (without shedding their larval skins).
- Upon pupation of the host, stylopid larvae migrate to the abdomen of the bee, eventually pupate in such a way that their heads end up protruding when the bee emerges.


Female stylopids are legless, wingless and soft-bodied and remain within the abdomen of the host for their entire lives.
Male stylopids emerge from the pupae as **winged adults** and **fly off to find another infected bee.** This leaves a gaping hole in the bee, killing it shortly after.
© Ed Phillips

- Female stylopids use pheromones to signal to males – they alter host bee behaviour causing it to climb high up on vegetation and sit there while the stylopid advertises her sexual receptivity.
- Mating occurs by a male jumping onto an infected bee and injecting sperm into the female stylopids neck region.
- Eggs hatch inside the female stylopids body and the triungulins leave through genital openings on the underside of their mothers body – eventually ending up on flowers as the bee forages where they wait to find a suitable bee that can take them back to a nest.

Infected bees **do not reproduce**, **have extended periods of activity** (emerge alongside males) and **often become intersexes.**

Brood-parasites of solitary bees

Scuttle flies (Phoridae) – some UK species lay their eggs in the nest provisions.

Sapygid wasps (2 UK species)

Other bees – ¼ of all bees in Europe and 13% of bee species worldwide are brood-parasites!

Some *Sphecodes* have been known to kill host females.

Brood-parasitic bees

Nomada rufipes

- Diversity and abundance may be a good indicator of the ‘health’ of entire bee community.
- **Generally heavily armoured**.
- Females have a modified reproductive track that allows them to **lay numerous eggs per day**.
- Can use **chemical mimicry** (masking their odours) to gain entry into host nests (e.g. in *Nomada*).
- Females may be capable of learning the location of host nests.
- **Can use chemical warfare** – some *Sphecodes* use pheromones to disorientate their hosts when in communal or eusocial nests.

- Three distinct modes of brood parasitism:

  - Adult, closed-cell (AC) = parasitic female locates a *closed, fully-provisioned brood cell*, gains access and **adult kills the host** egg/larva using its mandibles or sting. An egg is then laid into the brood cell and cell is closed.

  - Larval, closed-cell (LC) = parasitic female locates a *closed, fully-provisioned brood cell*, and deposits its own egg via a small opening before closing the cell. **Larval instar(s)** then **kill the host** egg/larva and co-occuring larvae (often using large mandibles).

  - Larval, open-cell (LO) = parasitic female lays eggs discretely into *open, partially provisioned brood cells*. Host egg is often small, asymmentrical and cryptically sculptured to avoid detection. **Larval instar(s)** then **kill the host** egg/larva and co-occuring larvae (often using large mandibles). *Nomada, Stelis* and *Coelioxys.*

Parasitoids of bees

- Majority of British thick-headed flies (**Conopidae**) are parasitoids of adult bees (solitary and bumblebees).
- Female ambushes an adult bee and **injects an egg into the abdomen**.
- Larvae then **develops inside** the bee for some time before **killing it, consuming all internal organs**.
- It then exists the host and moves into the lateral tunnels of the nest where it pupates.

Sicus ferrugineus

Parasitoids of bees

Leucophora © Katja Schulz

Satellite flies (Anthomyidae and Miltogramminae) lay their eggs on the nest provisions.

Mutilla europaea © Steven Falk

Velvet ant larvae eat bee prepupa/pupa in bumblebee nests.

Parasitoids of solitary bees

Bee-flies

Bombylius major

Mites that kill bee egg or larva – no competition for pollen/nectar or for the fungi that develops on the provisions

Ruby-tailed wasps

Yeasts and fungi can be major source of mortality in solitary bees (common in floral nectar)

Mutualistic (beneficial)

- Yeasts on the provision masses that may act as an **additional food source**, or **control competing and/or spoilage microorganisms**.
- Bacterial strains that: ← Passed from **mother to daughter** in honeybees and bumblebees, or acquired from the **environment**
  - contribute to the **conversion of nectar to honey**
  - **protect stored honey** (in honeybees and bumblebees)
  - **defence against pathogenic or spoilage microorganisms**
  - **fermentation of provision mass**
- Mites that feed on fungi, nest wastes or other mites.

Commensal nematodes

- **Feed on bacteria, yeasts and fungi**.
- Reported in **6 of 7 bee families** (except Stenotritidae).
- Commonly associated with social halictids (why?) and genera such as *Andrena*, *Anthophora* and *Colletes.*
- When mother coats a brood cell with Dufour's gland secretions, nematodes are transmitted to the brood cell where they feed on yeast and bacteria. Once bee moults to adulthood, juvenile nematodes moult to dauer stage (mon-feeding resting stage) and enter Dufour's gland (females) or genitalia (males).
- **Transmition largely vertical** (mother to son/daughter) but can **also occur through mating** (since males host nematodes in their genitalia!).

Commensal mites

© Matt Cole

Mites

- Associated with every bee family except Melittidae.
- **Vast majority are fungal feeders** and have no impact or are beneficial.
- Where mites are beneficial, females support specialised structures (acarinaria) for transporting them.
- Commonly **transferred during copulation** (male to female).
- **Brood parasitic bees can serve as vectors** for mites in the nests of their host.

Some carry fungal spores within specialised pouches, kill the host bee larva and then inoculate the brood chamber and provision mall with the fungus. Without the bee, the fungus grows rapidly and the frugivorous mites multiply!

These rarely act in isolation

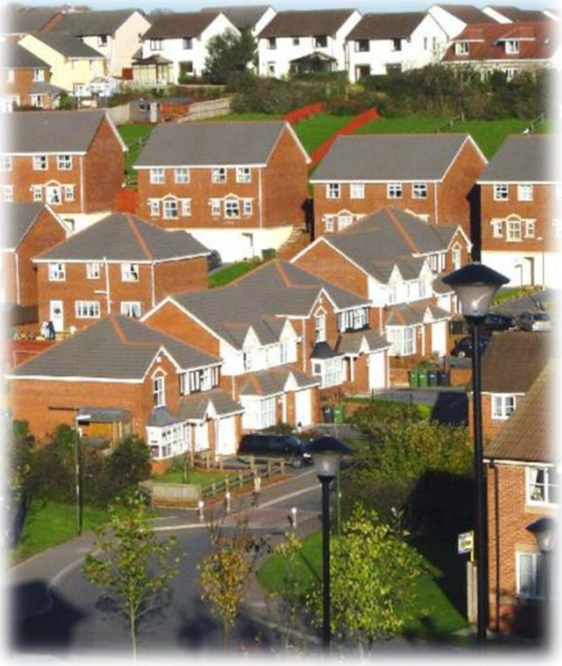
Threats to bees

1. **Habitat loss, fragmentation and degradation**
2. **Pesticides and pollution** → neonicotinoids
3. **Non-native species** (plants and animals)
4. **Disease** → most evidence indicates that the source is managed honeybees
5. **Climate change** → phenological mismatch

57% of all European bee species lack sufficient information to establish their status and 79% have unknown population trends.

1. Habitat loss, fragmentation and degradation

- **Single greatest impact on bee populations** – anthropogenic changes are not always detrimental however!
- **Host-plant specialists** are generally **most severely impacted** by habitat alteration.



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- In 1700, 11% of land on Earth was being used for agriculture – **now 40%**.
- Agricultural ecosystems are generally **much simplified** compared to the ecosystems they replace and bee communities generally **less abundant** and **less species-rich**.

2. Pesticides

- At individual level = **lethal effects** (direct mortality) and **sub-lethal effects** (effects on foraging, memory, learning and reproductive success).
- At community level = effects on **abundance and species-richness.**

2. Pesticides

- Pesticide exposure has been shown to **impair nest-finding ability, reduce offspring production, cause male-biased offspring production, and supress foraging activity.**
- Pesticide application can cause dramatic declines in wild bee abundance and species richness.
- Honeybees are widely used to measure 'bee toxicity' for virtually all pesticides (LD50 value) – but **honeybees may not provide a good measure of toxicity to bees in general.**
- **LD50 values may underestimate the toxicity to bees** when diverse chemicals are applied in combination.
- **Adjuvants** (added to pesticide mix to boost efficacy or provide better binding to plant substrates) **are not evaluated for direct toxicity**.

3. Non-native species

- Non-native plants **displace native flora**.
- Non-native plants can **allow social bees to persist in areas where they would normally be absent or rare** – increasing probability of competition with native solitary bees.
- **76 invasive bee species worldwide** (as of 2017) – majority are above-ground cavity or wood nesters that have been spread through international trade.
- Non-native bees can **compete with native bees** for floral and nesting resources, **transfer pathogens** to native species, and **disrupt reproduction** via interspecific mating.

Honeybee (*Apis mellifera*)

- The **most widespread and abundant non-native bee on Earth**!
- Has colonies of **tens of thousands of workers**, is **broadly polylectic** (visits virtually any flower), and **consumes vast quantities of pollen and nectar**.
- Over a 3 month period in peak summer, a single colony can consume enough pollen to support approximately 110,000 solitary bee offspring!
- Native bees may alter their foraging to avoid competition with honeybees.

4. Disease

- **Managed honeybee colonies are loaded with pathogens** (fungi, bacteria, viruses, microsporidia, trypanosomes).
- Increasing evidence that **honeybees** (and managed bumblebees) are a **source of pathogens** for wild bee species.
- Pathogen **transmition occurs via flora visitation**.
- Little is known about the impacts of pathogen infection on wild bees but it is clearly a threat.

5. Climate change

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- **Likely to impact bees in 3 ways:**

  – **Alter geographical distribution** of species, potentially leading to substantial range reductions or fragmentation of populations.
  – **Physiological effects on plants** (changes to quantity and quality of floral resources; no. and size of flowers; floral scent production; flowering times**) and bees** (body size; lifespan; flight, foraging and overwintering capabilities).
  – **Disrupt temporal synchrony between flowering and bee activity**.

Why are wild bees important?

- Reproduction of **~85% of all wildflower and flowering crop species** depends on, or is enhanced by, pollinators.
- Effective pollination is **crucial for human nutrition and food security**.
- Insect pollination **worth £690 million per annum** in the UK.
- Important in **maintaining and improving the yield and quality** of many fruit and vegetable **crops**.


“Wild pollinator declines beyond a critical threshold could trigger plant population decline or extinctions, in turn affecting the structure and composition of natural plant communities and ecosystems”


Thank you!
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