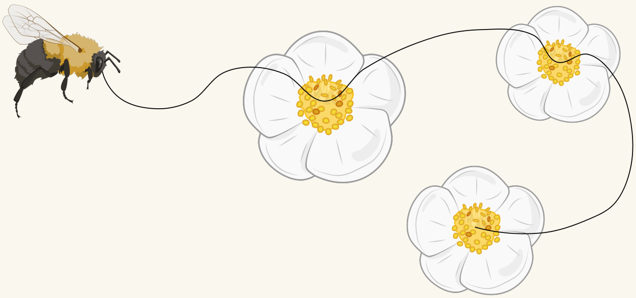
Bee in Motion

Modelling Bees' Movements



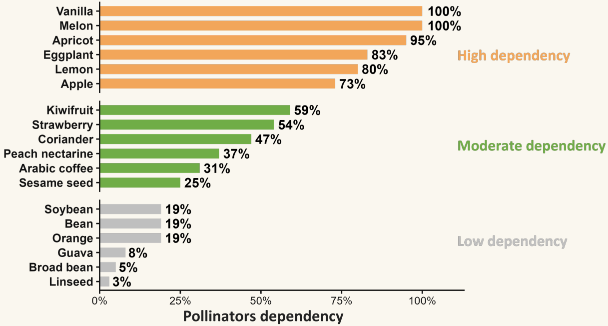
Apolline LOUVET & Quentin PETITJEAN

Probability Meets Biology III

INRAE

CONTEXT

Pollinators support >85% of flowering plants

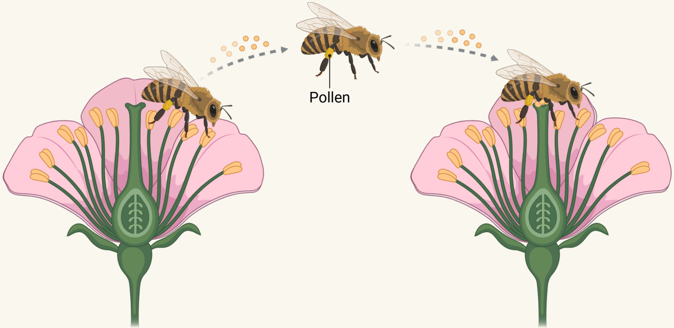


Pollination sustains biodiversity and food production.

Ollerton et al., 2011. Oikos; Siopa et al., 2024. Journal of Applied Ecology.

CONTEXT

Pollination is a movement-mediated process

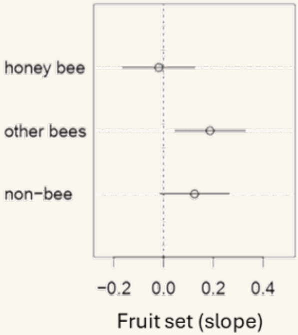


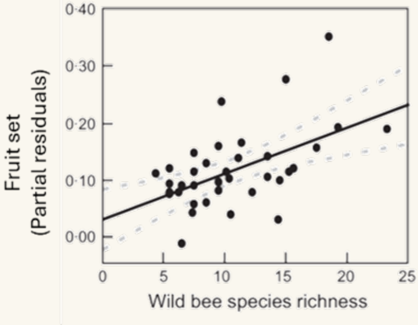
Pollen does not move by itself, it is mostly carried through sequences of flower visits.

Hung et al., 2023. Ecological Applications.

CONTEXT

Bees are among the most important pollinators





Wild bee diversity increases fruit set through complementary roles.

Mallinger & Gratton 2015. Journal of Applied Ecology; Rader et al., 2016. PNAS.

CONTEXT

Bee size changes movement and floral contact

Body size affects both how far bees move and how their bodies contact floral reproductive organs.

CONTEXT

Bee diversity is multidimensional









Bees also differ in nesting biology, sociality, floral specialization, cognition, and flower-use strategies.

CONTEXT

Specialisation changes movement patterns

The Bryony mining bee (*Andrena florea*)
(Short tongue - monolectic)

Bryony (Bryonia dioica)
(male and female flowers on different plants)

A short-tongued, monolectic bee mainly moves within the spatial network of its host plant.

CONTEXT

Long-tongued bees can access deep flowers

The Garden bumblebee (*Bombus Hortorum*)
(Long tongue - polylectic)

Sage (*Salvia sp.*) and Clover (*Trifolium sp.*)
(Very deep flower)

Morphological matching between tongue length and flower depth determines which flowers are visited.

CONTEXT

Bee species do not move in the same way

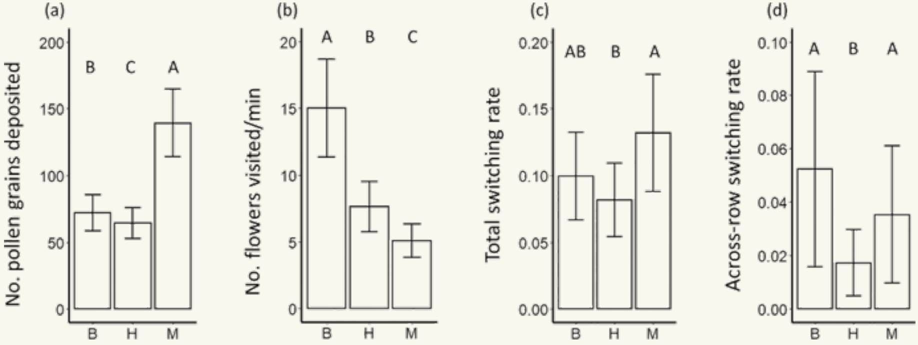
	Bumble bee	Honey bee	Leafcutting bee
Direction	More directional	Somewhat directional	Nearly random
Distance	Depends on # flowers visited	Depends on # flowers visited	Independent of # flowers visited
Best model	Modelled distance + direction	Less clear	Random-like direction

Different bee species may disperse pollen differently.

Brunet et al., 2023. Scientific Reports.

CONTEXT

Bee species do not visit flowers in the same way

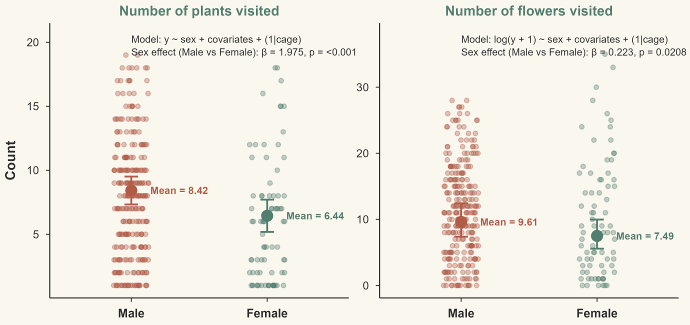


Mining bees visit fewer flowers but deliver more pollen per visit.

Hung et al., 2023. Ecological Applications.

CONTEXT

Sex can shape the visitation patterns

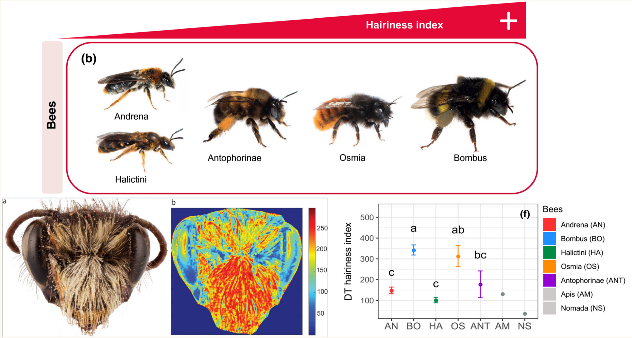


Males visit more plants and flowers than females.

Petitjean et al., Unpublished data.

CONTEXT

Hairiness changes pollen transport



Hairiness varies among bee taxa and between sexes, affecting pollen pickup, carryover and deposition.

Stavert et al., 2016. PeerJ; Roquer-Beni et al., 2020. Ecology and Evolution.

GAPS

Existing models rarely connect all scales

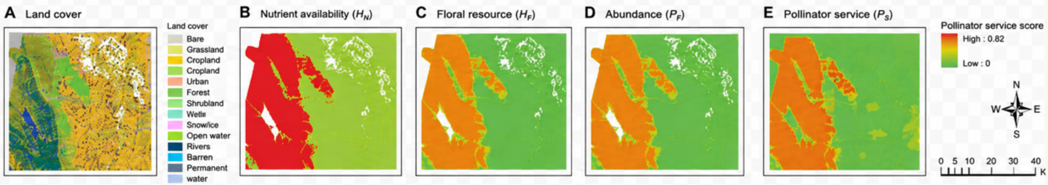
- Pollination models often simplify movement as distance-based dispersal.
- Behavioral models can include learning, memory, exploration, and trapline formation.
- But the full link from bee traits to movement rules to pollen flow remains difficult to formalise.

How do individual movement rules scale up to plant-level pollination patterns?

Mailly et al., 2025. Frontiers in Ecology and Evolution; Mailly et al., 2025. Integrative and Comparative Biology.

EXAMPLE #1

Pollination model: INVEST

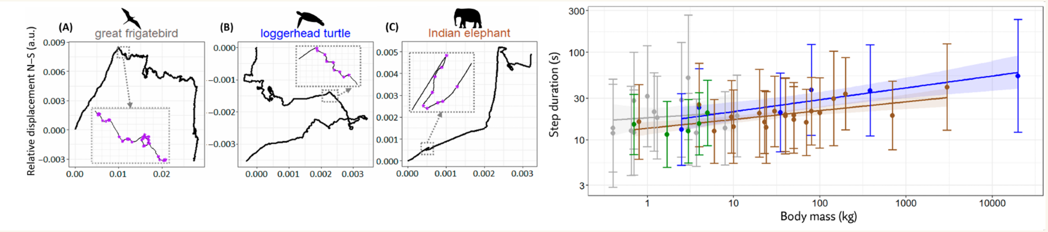


Predict where pollinators are likely to occur, not how they move between flowers.

Lonsdorf et al., 2009. Annals of Botany.

EXAMPLE #2

Movement as steps and turns

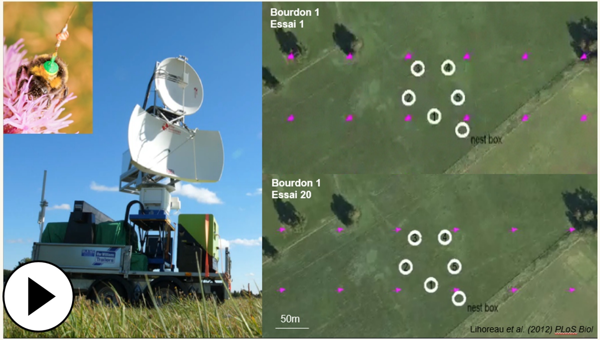


A trajectory can be decomposed into segments and decision points and linked to body mass.

Gunner et al., 2026. Ecological Monographs.

EXAMPLE #3

Traplines

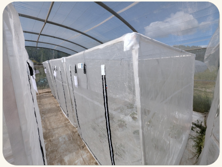


Bees rely on memory to move across flowers.

Lihoreau et al., 2012. Plos Biology; Woodgate et al., 2017. Scientific Reports.

NEXT STEP

Testable movement models





Beyond simulating bee movements, we need models whose assumptions and predictions can be tested experimentally.

Experimental setup: pesticide exposure, plants and flowers and 3D bee movement tracking.

SUMMARY
From biology to mathematics

- Plant reproduction depends on pollen transfer.
- Pollen transfer depends on the order of flower visits.
- Visit sequences depend on bee traits, cognition and the environment.

Bee traits $\longrightarrow$ Movement rules $\longrightarrow$ Visit sequences $\longrightarrow$ Pollen flow

Can we predict bee movement from biological traits?

HYPOTHESES

Which traits are expected to drive bee movements?

Trait / condition	Expected effect	Model parameter
Body size/mass	Larger bees may fly farther, faster, and turn less often.	Step length, speed, turning rate
Nectar/pollen load	Loaded bees may reduce exploration or return sooner to the nest.	Return probability, flight cost, persistence
Sociality/nesting	Central-place constraints differ between solitary and social bees.	Nest attraction, maximum range, bout duration
Floral specialization	Specialists may bias movement toward specific flower types.	Preference weights w_k, attraction kernel
Memory/learning	Previous rewards can reinforce profitable transitions.	Learning rate, memory window, exploitation
Hairiness	Mostly affects pollen pickup, carryover, and deposition.	Pollen load, deposition rate, carryover decay

MODELLING

Basic modelling components

- Bee paths can be divided into foraging bouts starting and ending at a central location (e.g., a nest).
- Flowers can be represented as patches containing a certain amount of nectar, which is regularly replenished if consumed by bees.
- During a foraging bout, bees move from one patch to another, until they have collected enough nectar or have flown for too long.

How do bees move from one flower to another ?

MODELLING BEE MOVEMENT

Example # 1 (Dorin et al., 2022. PLOS Sustain Transform)

At each timestep, the pollinator:

- Identifies all flower locations within a given radius, and moves to the closest one not recently visited.
- Decides whether to land on that flower depending on its species and the one of the flower most recently visited.
- If lands, pollinates the flower.
- If does not land, moves of a fixed distance in an uniform-random direction.

Stochastic components: whether to land on the closest flower identified, movement if deciding not to land

MODELLING BEE MOVEMENT

Example # 2 (Kortsch et al., 2023. Functional Ecology)

- Patch = plant species × flower density
- Pollinators are assigned random preferences for each plant species, and they rank plant patches according to preference × flower density
- Movement = correlated random walk (random turning angles), with foraging range and flight speed depending on bee characteristics, until it finds plants.
- Once pollinator finds plants, it chooses the most attractive one.

Stochastic components: plant species preferences, pollinator movement

MODELLING BEE MOVEMENT

Example # 3 (Newton et al., 2018. PLOS One)

- Each bee species is associated to a list of plant species they can pollinate, and a maximal distance they can fly ($\approx$ energy level)
- Bee movement = correlated random walk (random turning angles), with steplength following a normal distribution
- When entering a patch of plants they can pollinate: ✓
- No choice between different plant options

Stochastic components: Pollinator movement

MODELLING BEE MOVEMENT

Summary: Movement models

Model	Movement rule	Biological interpretation
Random walk	Next step independent of direction and memory.	Naive exploration.
Correlated random walk	Direction persists between steps.	Directional movement/inertia.
Biased walk	Movement biased toward resources or cues.	Sensory perception, floral attraction.

Aim #1: How to differentiate between these different models given empirical movement data ? How to link movement parameters and biological traits ? How to define a minimal mathematical framework for bee movement among flowers ?

MODELLING BEE MOVEMENT

Other possible movement models ?

Model	Movement rule	Biological interpretation
Random walk	Next step independent of direction and memory.	Naive exploration.
Correlated random walk	Direction persists between steps.	Directional movement/inertia.
Biased walk	Movement biased toward resources or cues.	Sensory perception, floral attraction.
Reinforced walk	Previously rewarding transitions become more likely.	Learning and memory.
Trapline	Repeated sequence of profitable sites.	Emergent route optimization.

Integration of learning processes, supported by experimental data

MODELLING BEE MOVEMENT

What is traplining ?

Traplines are stable sequences of familiar feeding sites visited by a bee during each foraging bout, as a result of reinforcement learning.

- Lihoreau et al., 2012. PLoS Biol: compares net length of route just travelled to shortest route experienced so far.
- Le Moël et al., 2019. Front Psychol: "vector-based learning"
- Dubois et al., 2021. PLoS Comput Biol: Same idea, based on a distance-based probability matrix, modulated each time the bee finds the flower rewarding (positive reinforcement) and/or unrewarding (negative reinforcement)

MODELLING BEE MOVEMENT

Example # 4 (Mailly et al., 2025, Integrative and Comparative Biology)

- Each transition from plant A to B has perceived value $=$ nectar available $\times$ "reachability"
- Expectation of plant-to-plant transition value updated each time this transition is realized, by a weighted average of the current and previous perceived values
- Next plant to visit according to probabilities weighted by the expected transition value

Stochastic component: Transition from one flower to another

MODELLING BEE MOVEMENT

Example # 5 (Dubois et al., 2021)

- Initialisation with matrix of movement probabilities
- (Positive reinforcement) If transition leads to rewarding flower, multiply transition probability by 1.5, and renormalization
- (Negative reinforcement) If transition leads to unrewarding flower, multiply transition probability by 0.75, and renormalization
- Flower nectar is refilled between foraging bouts

$\Longrightarrow$ Strong link with reinforced random walks

MODELLING BEE MOVEMENT

More about traplining (mostly from Dubois et al., 2021)

Experimental results

- Not all pollinators exhibit traplining $\Longrightarrow$ Dependance on species traits ?
- Within one pollinator species, not all individuals exhibit traplining $\Longrightarrow$ Stochastic component ? Dependance on individual traits ?

Simulation results

- Fastest trapline development when only positive reinforcement
- No observed convergence to a trapline when only negative reinforcement
- Combination of positive and negative reinforcement maximizes patch exploration

FROM BEES TO PROBABILITY

Traplining as convergence of a stochastic process

The sequence of foraging bouts can be interpreted as a (discrete-time) stochastic process taking its values in the space of finite excursions from the origin

(+ information on the transition matrix ?)

"traplining"

=

convergence of any realization of the stochastic process to a limiting "stable" excursion (which might differ from one realization to another)

FROM BEES TO PROBABILITY

Traplining as convergence of a stochastic process

Experimental results

- Not all pollinators exhibit traplining $\Longrightarrow$ Dependance on species traits ?

  Under which conditions on model parameters can we observe traplining ?

- Within one pollinator species, not all individuals exhibit traplining $\Longrightarrow$ Stochastic component ? Dependance on individual traits ?

  Does convergence occurs "almost surely" or with probability bounded away from 1 ?

  Is the limiting excursion deterministic or a random variable ?

FROM BEES TO PROBABILITY

Traplining as convergence of a stochastic process

Simulation results

- Fastest trapline development when only positive reinforcement

  What is the speed of convergence to the limiting trapline ?
- No observed convergence to a trapline when only negative reinforcement

  Under which conditions on model features do we observe traplining ?
- Combination of positive and negative reinforcement maximizes patch exploration

Aim # 2: Understand the drivers of the emergence of traplines, and derive theoretical predictions on species traits related to traplining.

DISCUSSION
Opening questions

- Which biological traits should considered in a movement model?
- What is the simplest stochastic process that still captures bee movement diversity?
- Which empirical data would be needed to identify and validate the model?

TAKE-HOME

Pollination patterns emerge from movement rules

To predict pollen flow, we need to model bees in motion.

- Bee traits shape movement rules.
- Movement rules shape visitation sequences.
- Visitation sequences shape pollen transfer and plant reproduction.