The visual ecology of bees - Tales of diverse eyes and behaviours

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2021

Citation for published version (APA):
Tichit, P. (2021). *The visual ecology of bees - Tales of diverse eyes and behaviours*. [Doctoral Thesis (compilation)]. MediaTryck Lund.

Total number of authors:
1

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The visual ecology of bees

Tales of diverse eyes and behaviours

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DOCTORAL DISSERTATION

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To be defended in the Blue Hall, Ecology Building, Sölvegatan 37, Lund, Sweden.
On Friday 23th April 2021 at 09:00

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Bristol, United Kingdom

Organization
LUND UNIVERSITY
Departement of Biology
Sölvegatan, 35, 22 362
Lund Sweden

Document name

DOCTORAL DISSERTATION

Date of issue 2021-03-15

Author Pierre Tichit

Sponsoring organization

Title and subtitle The visual ecology of bees – Tales of diverse eyes and behaviours

Abstract

With about 25 000 species, bees form a very diverse group of insects with a vast behavioural repertoire and range of habitats. Bees rely heavily on their eyes for most behaviours, including controlling their flight, navigating, foraging and finding mates. Investigating the diversity of the visually-guided behaviours and visual systems in bees allows us to understand how they interact with their environment across space and time.

In this thesis, I focused on different aspects of the visual ecology of bees in order to understand how the variety of bee ecology and behaviour interplays with the diversity of their visual system. In chapter one, I discovered a new landing behaviour in a species of stingless bee that may be shaped by ecological factors. I then showed in chapter two that bees use a simple visual-based mechanism to control this landing behaviour. In chapter three, I co-developed a new method for analysing visual systems that sets the groundwork for a comprehensive understanding of the diversity of the compound eyes in bees. Finally, I discovered in chapter four that the lifestyle and habitat of bumblebees may have driven the diversification of their eye.

The results of this work reveal the tight links between the diverse eyes, behaviours and ecologies of bees. They contribute to answering fundamental questions about the evolution of animal eyes and behaviours and, by revealing new information about the visual biology of bees, could also support their conservation.

Key words animal behaviour, arthropods, bumblebees, compound eyes, crystalline cones, flight control, image analysis, landing, sensory ecology, stingless bees, vision, X-ray microtomography

Classification system and/or index terms (if any)

Supplementary bibliographical information

Language English

ISSN and key title

ISBN
print 978-91-7895-785-9
pdf 978-91-7895-786-6

Recipient's notes

Number of pages 231

Price

Security classification

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Date 2021-03-10

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Cover illustration by Mai Hatano

Faculty of Science
Department of Biology

ISBN (print) 978-91-7895-785-9
ISBN (pdf) 978-91-7895-786-6

Printed in Sweden by Media-Tryck, Lund University
Lund 2021

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MADE IN SWEDEN

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II. **Tichit P**, Alves-dos-Santos I, Dacke M, Baird E. 2020 Accelerated landings in stingless bees are triggered by visual threshold cues. Biology Letters. 16.

III. **Tichit P**, Zhou T, Kjer HM, Andersen Dahl V, Bjorholm Dahl A, Baird E. 2020 *InSegtCone*: Interactive Segmentation of crystalline Cones in compound eyes. bioRxiv. *(submitted)*

IV. **Tichit P**, Bodey A, Rau C, Baird E. 2021 'Same same but different': exploring evolutionary and ecological causes of eye diversification in bumblebees. *(manuscript)*

Author contribution

- **Pierre Tichit** designed the study together with Emily Baird and Isabel Alves-dos-Santos. **Pierre Tichit** carried out the collection and processing of behavioural data. **Pierre Tichit** performed the analysis of behavioural data and interpreted it with Emily Baird. **Pierre Tichit** designed the mathematical simulations with input from Emily Baird. **Pierre Tichit** wrote the manuscript with the support of Emily Baird.
- **Pierre Tichit** designed the study together with Emily Baird and Isabel Alves-dos-Santos. **Pierre Tichit** carried out the collection and processing of behavioural data. **Pierre Tichit** interpreted the data with the help of Emily Baird. **Pierre Tichit** wrote the manuscript with the support of Emily Baird.
- **Pierre Tichit** designed the study together with the other authors. **Pierre Tichit** collected the data and generated the analyses in collaboration with Tunhe Zhou and Hans Martin Kjer. **Pierre Tichit** interpreted the data and wrote the manuscript in close collaboration with Tunhe Zhou.
- **Pierre Tichit** designed the study and carried out the collection of samples with the help of Emily Baird. **Pierre Tichit** prepared the samples and contributed to sample imaging together with the other authors. **Pierre Tichit** performed the volumetric, computational and statistical analysis. **Pierre Tichit** interpreted the data and wrote the manuscript with minor input from Emily Baird.

Papers not contained in this thesis

- Taylor GJ, **Tichit P**, Schmidt MD, Bodey AJ, Rau C, Baird E. 2019 Bumblebee visual allometry results in locally improved resolution and globally improved sensitivity. eLife 8.
- Wilby D, Aarts T, **Tichit P**, Bodey A, Rau C, Taylor G, Baird E. 2019 Using micro-CT techniques to explore the role of sex and hair in the functional morphology of bumblebee (*Bombus terrestris*) ocelli. Vision Research. 158, 100-108.
- Baird E, **Tichit P**, Guiraud M. 2020 The neuroecology of bee flight behaviours. Current Opinion in Insect Science.
- Jezeera A, **Tichit P**, Kelber A, Somanathan H. Eye structure and spatial resolution in the stingless bee *Tetragonula iridipennis*. *(in preparation)*

Encounter with a friendly male bumblebee during a day of collecting in northern Sweden (2019).

Popular summary

The buzzing flight of bees is a popular summer hit. Yet, outside of a few familiar species of honeybees and bumblebees, these fantastic little creatures are still mostly unknown. With about twenty-five thousand species, bees are a very diverse group. They can be found in drastically different habitats. For example, some kinds of bumblebees endure the freezing temperatures and windswept tundra of Greenland, while others only thrive in the heat and humidity of the Amazonian forest. Some bees live in huge colonies with tens of thousands of members, while others live solitary lives. Some are narrower than a sesame seed, while others can reach the size of a human thumb. Despite these differences, bees all have in common the urge to visit flowers where they find their food. This habit makes them very important for the pollination of plants across the world. To go about their laborious life, bees make extensive use of their vision. They possess two types of eyes – ocelli and compound eyes – that they use to control their flight, find their way through the world, discover flowers and spot possible mates. To understand how bees interact with the environment, we thus need to explore the diversity of their eyes and of how they use them.

The first chapter of my thesis is about landing, which is a fundamental behaviour in flying insects. However, in bees it is poorly known whether different species land in different ways. During an expedition to Brazil, I came across a species of bee with the most peculiar landing style. Rather than slowing down to land, as most animals do, these bees accelerate just before touchdown on the entrance to their hive. Why do these bees speed up when they land? Using a computer simulation, I found that this weird strategy may help the bees to avoid mid-air collisions with nestmates and reduce bee ‘traffic jams’ in front of the hive. In turn, this would make food collection more efficient for the colony and it would be easier for hive members to defend against intruders. With this chapter, I showed that the lifestyle of bees – where they live, how many there are and if they are exposed to intruders – can strongly influence their behaviour.

In chapter two, I then asked if and how the bees from chapter one use vision to control their peculiar landing. I found that they did indeed rely on vision to control their landing and that they did so in a simple manner. Essentially, when the image of the entrance of the hive reaches a given size on their eyes, these bees start to speed up. When the image of the entrance reaches a second set size on the eyes of landing bees, they extend their landing gear – which is, for bees, their legs – in preparation for touchdown.

This chapter reveals that bees can use simple rules to achieve complex behaviours such as landing safely.

To explore the diversity of eyes in a large number of bees, we use X-ray images taken from a sample as it rotates (an approach known as computed tomography or CT, commonly used in a medical setting) to produce 3D images of the eyes. However, powerful tools are needed to analyse the large amounts of data that this approach generates. As I want to better understand how bee eyes work, I needed an efficient method for analysing 3D eye images created by CT, so I developed an automatic tool for distinguishing essential optical structures in the eyes of insects and other arthropods. In chapter three, I describe this method, provide a guide to use it, and give examples of its application to a few insect eyes.

In the last chapter, I used CT to look into the diversity of the eyes across a range of bumblebees from different habitats around the world. Even though different species are genetically close to each other, I found that their eyes were far from ‘all the same’. For example, bumblebees that live in forests have eyes that may enable them to see less sharp but better in dim light than bumblebees living in open landscapes. I also found that cuckoo bumblebees – bees that lay their eggs in another bumblebee hive like cuckoo birds do – had peculiar eyes in comparison to other bumblebees. This indicates that the eyes of each species of bumblebees may be specialised for a specific combination of lifestyle and habitat. These results are important for the conservation of bumblebees because they suggest that the eyes of some species may make them more sensitive than others to changes in the environment. For example, farming practices that create large open fields may particularly disadvantage bumblebees with eyes adapted to forests.

These four chapters only scratch the surface of the tight links between the eyes of bees, the ways they behave, and the worlds they live in. I hope that efforts to look into their diverse eyes will continue and will help to protect these crucial but endangered animals.

Populär sammanfattning

Binas surrande är en viktig komponent för känslan av sommar. Men, förutom många hyllmeter av litteratur om några vanliga arter av honungsbi och humlor, vet vi än idag förvånansvärt lite om många av de tjugofem tusen arter vi kallar bin. Vissa humlor överlever Grönlands minusgrader och hårda vindbyar, medan de i Amazonas snarare älskar skogens höga temperatur och fuktighet. Vissa arter bor i stora bon tillsammans med flera tusen individer, andra lever ensamma. Några är mindre än ett sesamfrö, någon lika långa som en tumme.

Trots dessa olikheter, delar de en stark och gemensam lust av att besöka blommor för att hitta föda. Därför är de så viktiga för att pollinera växter runt jordklotet. För att leva sina korta liv använder bina framför allt sina ögon. De har två slags ögon, punkt- och facettögon, som de använder för att säkert flyga, navigera, hitta blommor och upptäcka andra individer för att para sig med.

Avhandlingens första kapitlen handlar om landning. Att kunna landa är en grundläggande förmåga för flygande insekter, men det är i stora drag okänt hur olika arter av bi bemästrar detta. Under en fältresa till Brasilien stötte jag på ett bi med en mycket underlig landnings-stil. I stället för att sakta ner för att landa – som de flesta andra djur inte oväntat gör – accelererade dessa bin strax innan de landade på boets ingång. Varför gasade de på detta sätt? Med hjälp av en datorsimulering kunde jag visa att denna märkliga strategi troligen hjälper bina att inte kroka mot varandra i luften och minskar risken för ”bitrafikstörning” framför boet. Detta kan i sin tur förbättra kolonins kapacitet att samla föda och försvara boet mot inkräktare. I kapitel ett diskuterar jag hur bins livsstil (dvs var de bor, hur många de är och hur känsliga de är för inkräktare) kan påverka deras beteende.

I kapitel två tittar jag djupare på hur dessa ”snabblandande” bin använder sina ögon för att styra denna ovanliga landningsstrategi. I dessa studier upptäckte jag att bina börjar accelerera när bilden på boets ingång når en specifik storlek i deras ögon. Så snart bilden på boets ingång når en annan given storlek fäller de snabbt ut sitt landningsställ, dvs sina ben, för att slutligen landa. Resultaten visar tydligt hur bin kan följa mycket enkla regler för att styra komplicerade och viktiga beteende.

Jag och många andra forskare använder idag röntgen som strålas på ett roterande prov för att producera en 3D-bild av det samma (detta är en teknik som kallas röntgentomografi och har länge använts för diagnostik inom vården). Problemet är att det krävs effektiva algoritmer för att kunna analysera den enorma mängd data som denna teknik genererar. Inom ramarna för att förstå hur ögonen hos bin är uppbyggda, utvecklade jag en snabb metod för att möjliggöra en 3D- analys av röntgentomografiska bilder av denna typ av små, biologiska prov. I avhandlingens tredje kapitel beskriver jag det verktyg jag utvecklat för att automatiskt identifiera viktiga optiska komponenter hos ett insektsöga.

I avhandlingens sista kapitlen presenterar jag hur röntgentomografi kan användas för att utforska mångfalden i ögonegenskap hos humlor som bor i olika miljöer. Även om många av dessa arter var mycket nära släkt, kunde jag utifrån dessa 3D-studier visa att deras ögon skilde sig åt i flera aspekter. Till exempel humlor som lever i skogar har ögon som troligen gör att de ser suddigare – men bättre i mörker – än humlor från öppna landskap. Jag hittade också att snylthumlor (de liknar gökar i och med att de lägger ägg i andra humlornas bo) har distinkta ögon jämfört med andra humlor. Sammantaget pekar min studie mot att ögonen hos var humlaart är nära anpassad till en given kombination av livsstil och miljö. Detta tyder in sin tur på att vissa arter, utifrån hur deras ögon är uppbyggda, är känsligare inför snabba omvärlds-förändringar än andra. Till exempel kan landbruksvanor som skapar ett öppet landskap bli särskilt skadliga för humlor med skogsanpassade ögon.

Denna avhandling är ett litet, men viktigt, steg mot ett djupare förståelse för de nära kopplingarna som finns mellan bins syn, beteende och dess omvärld. Jag hoppas att min avhandling kommer att inspirera andra att forska vidare inom detta ämne, och att de resultat som kommer fram kan hjälpa oss att bevara denna hotade grupp av insekter.

Résumé vulgarisé

Le bourdonnement des abeilles a toujours été l'un des tubes de l'été les plus populaires. Cependant, mis à part les quelques espèces d'abeilles à miel et de bourdons les plus communes, on sait encore très peu de choses sur ces fabuleuses petites bestioles. Il y a environ vingt-cinq mille espèces d'abeilles dans le monde, présentes dans une multitude d'habitats. Par exemple, certaines espèces survivent aux températures extrêmes et aux vents violents des toundras du Groenland, tandis que d'autres ne se plaisent que dans la chaleur moite de la forêt amazonienne. Certaines abeilles forment d'immenses colonies comptant des dizaines de milliers d'individus ; d'autres vivent des vies solitaires. Les plus petites ne sont pas plus larges qu'une graine de sésame ; alors que les plus grandes font la taille d'un pouce.

Malgré ces différences, toutes les abeilles ont un instinct commun : visiter des fleurs pour y trouver leur nourriture. C'est pour cela que les abeilles sont extrêmement importantes pour la pollinisation des plantes ! Pour mener leur vie de labeur, les abeilles comptent beaucoup sur leur vue. Elles possèdent deux types d'yeux qu'elles utilisent pour contrôler leur vol, trouver leur chemin à travers le monde qui les entoure, découvrir des fleurs et repérer des partenaires sexuels potentiels. Pour comprendre comment les abeilles interagissent avec leur environnent, il est donc nécessaire d'explorer la diversité de leurs yeux et des utilisations qu'elles en ont.

Le premier chapitre de ma thèse traite de l'atterrissage. En effet, pour tout insecte volant qui se respecte, savoir atterrir sans dommage est essentiel. Cependant, peu de recherches ont été menées chez les abeilles afin de savoir si différentes espèces atterrissent de différentes manières. Au cours d'une expédition au Brésil, j'ai fait la rencontre d'une espèce d'abeille avec un style d'atterrissage très inhabituel. Au lieu de ralentir comme la plupart des animaux le font, ces abeilles accélèrent juste avant de rentrer en contact avec l'entrée de leur nid. Pourquoi ces abeilles accélèrent-elles pendant l'atterrissage ? Grâce à une simulation, j'ai trouvé que cette stratégie étrange pourrait permettre aux abeilles d'éviter les accrochages aériens avec les autres individus de la même colonie et de limiter les « bouchons » devant l'entrée du nid. En retour, cela permettrait à la colonie d'effectuer une collecte de nourriture plus efficace et la rendrait plus facile à défendre contre les intrus. Dans ce premier chapitre de ma thèse, j'ai donc montré comment le mode de vie des abeilles (c'est à dire où elles habitent, combien elles sont, et si elles sont exposées aux intrus) peut avoir une forte influence sur leur comportement.

Dans le deuxième chapitre, je me suis demandé si ces mêmes abeilles comptaient sur leur vue pour contrôler leurs atterrissages atypiques, et si oui, comment. J'ai démontré qu'elles utilisent effectivement leur vue pour contrôler leurs atterrissages, et pour ce faire, qu'elles font appel à une stratégie assez simple. Pour résumer, quand l'image de l'entrée de leur nid atteint une taille donnée à leurs yeux, les abeilles commencent à accélérer. Ensuite, lorsque l'image de l'entrée de leur nid atteint une seconde taille (environ trois fois plus grande que la première) à leurs yeux, elles déploient leur « train d'atterrissage » (c'est à dire leurs pattes) avant de « toucher la piste ». Ce chapitre révèle que les abeilles peuvent utiliser des règles simples pour guider des comportements complexes, en l'occurrence un atterrissage rapide mais sans encombre.

Afin d'explorer la diversité des yeux d'un grand nombre d'abeilles, j'utilise, avec d'autres chercheurs, des images obtenues grâce à des rayons X projetés sur un échantillon en rotation (cette technique s'appelle la tomographie à rayon X, et est couramment utilisée pour l'imagerie médical). Cela permet d'obtenir des images des yeux en 3D. Cependant, il manque des outils puissants pour analyser les quantités énormes de données que cette technique génère. Dans le but de comprendre comment les yeux des abeilles fonctionnent, il me fallait une méthode efficace pour analyser les images tridimensionnelles des yeux obtenues avec la tomographie à rayon X. J'ai donc développé un outil informatique pour délimiter de façon automatique certaines composantes optiques essentielles des yeux des insectes et d'autres arthropodes.

Dans le dernier chapitre, j'ai utilisé la tomographie à rayon X afin d'explorer la diversité des yeux au sein d'espèces de bourdons vivant dans différents habitats à travers le monde. Même si toutes ces espèces sont génétiquement proches les unes des autres, j'ai trouvé que leurs yeux sont loin d'être tous identiques. Par exemple, les bourdons vivant dans des forêts possèdent des yeux qui semblent leur permettre de mieux voir dans l'obscurité, mais plus flou que ceux vivant dans des endroits dégagés. J'ai aussi trouvé que les bourdons coucous, des espèces qui pondent leurs œufs dans le nid d'autres bourdons (de manière similaire aux oiseaux du même nom), avaient des yeux différents de ceux des autres bourdons. Cela indique que les yeux de chaque espèce de bourdons pourraient être adaptés à un mode de vie et un habitat spécifiques. Ces résultats sont importants pour la conservation des bourdons car ils suggèrent que les yeux de certaines espèces pourraient les rendre plus sensibles que d'autres aux changements environnementaux. Par exemple, il est possible que les pratiques agricoles qui génèrent des espaces ouverts soient particulièrement désavantageuses pour les bourdons dont les yeux sont adaptés aux forêts.

Ces quatre chapitres ne font qu'amorcer l'exploration des liens étroits qui existent entre les yeux des abeilles, leurs comportements et les endroits où elles vivent. J'espère que ces efforts se poursuivront et contribueront à protéger ces insectes essentiels mais menacés !

“I'm very slow, I'm very weak,
I'm often scared and I got no beak,
I got no sting, my teeth are small,
I don't know anything at all.

Don't touch my animals,
leave them alone
they're on their own,
don't touch my animals.”

Michael Schiefel

The scope of the thesis

Close your eyes and imagine, five hundred and fifteen million years ago, a shallow sea on what would later become southern Australia. Over the seabed, a 70 cm long Animalocaris is searching for prey. In fact, it is looking for prey, because already in the early Cambrian, this animal possessed, like many other arthropods, a pair of highly sophisticated compound eyes (Paterson et al., 2011). Since their emergence, nearly all phyla in the animal kingdom have evolved some type of visual organ. These are considered to be true eyes if they can distinguish light incoming from different regions in space (Land and Nilsson, 2012).

What is so good about having eyes? 'The world is what we perceive' (Merleau-Ponty, 1945), which implies that senses are the only way to get knowledge about what surrounds us. Eyes are particularly advantageous because they 'provide instantaneous and detailed information about the environment both close up and far away' (Land and Nilsson, 2012). The visual information that is then processed in the neural system provides the basis for many behaviours (Cronin et al., 2014) that benefit the animal by increasing its survival and/or number of offspring.

However, neural cells, and particularly the photoreceptors present in the eyes of animals, have a high energetic cost (Niven and Laughlin, 2008). As in the digital world, where growing file sizes require bigger storage centres and processing power, more sensory input demands a bigger brain (Axelrod et al., 2018). A consequence of these two phenomena is that animal eyes, especially in small-brained invertebrates, typically sample only a finite subset of the visual world such that most unnecessary information is filtered out (Wehner, 1987). Eyes have evolved to acquire the visual input necessary for producing the most adaptive behaviour whilst reducing the energetic costs incurred (Niven and Laughlin 2008). Because distinct behaviours require different sensory information and because the visual world varies widely in the availability and distribution of information, eyes have evolved in relation to the ecological needs specific to an animal - that is, its visual ecology - and are, as such, 'matched filters' (Wehner, 1987).

By studying how eyes and visual capacities are matched to the environment, visual ecologists can predict what elements of the visual world are necessary for performing or generating a behaviour which, in turn, can provide insights into how an animal interacts with its environment. Visual ecology can help us to understand abiotic or biotic interactions, and even spatiotemporal distribution, life history or social structure of populations and communities (Weissburg, 2005).

In my thesis, I focused on the visual ecology of bees. Bees form a very diverse group of visually-driven insects with a wide behavioural repertoire and ecological range, making them ideal models for answering fundamental questions in the study of eyes and behaviours. Moreover, it is crucial to explore the diversity of bee ecology and behaviour in order to develop efficient strategies for preserving them and their major contribution to the pollination of plants.

How does the variety of bee ecology and behaviour interplay with the diversity of their visual system? This central question is underlying the four chapters of this thesis. Throughout my research, I asked how the ecological context can shape bee behaviours (paper I), how bees use their eyes to control a behaviour (paper II), how the visual properties of bee eyes can be quantified (paper III), and if and how the diversity of visual systems interplays with ecological factors (paper IV).

I discovered a new landing behaviour in a species of stingless bee that may be shaped by ecological factors (paper I), and that bees use a simple visual-based mechanism to control this landing behaviour (paper II). I co-developed a new method for analysing visual systems that sets the ground for a comprehensive understanding of the diversity of bee eyes (paper III). Finally, I discovered that the lifestyle and habitat of bumblebees may have driven the diversification of their eye (paper IV).

Of course, these findings only scratch the surface of the tight links between the diverse eyes, behaviours and ecology of bees. However, they contribute to answering fundamental questions about the evolution of animal eyes and behaviours, and could also, by revealing new information about the biology of bees, support their conservation.

Summary of the chapters

Paper I

To land, flying animals must simultaneously regulate their speed and control their trajectory towards the target. Previous work on landing has shown that animals reduce their speed as they approach the target, but how widespread this strategy is remained understudied. To explore this, I recorded the stingless bee *Scaptotrigona depilis* landing on its naturally small hive entrance. Rather than slowing down as most animals do, I found that *S. depilis* accelerates just before touching down on its target. What could be the benefits of such a counterintuitive 'accelerated landing' strategy? Thanks to a simulation of landing traffic, I found that this strategy may reduce the risk of collisions and traffic congestion in front of the often-busy hive and thus improves food collection and nest defence. This work brings to light the diversity of landing behaviours and how they may be shaped by the ecological context of a species.

Paper II

In this chapter, I investigate if and how the stingless bee *Scaptotrigona depilis* uses visual cues to control the 'accelerated landing' it typically makes when approaching its hive entrance. Whereas previous work investigated landing control in animals that decrease speed prior to touchdown, the present study is one of the first to focus on landing control in a species that accelerates during landing. I found that *S. depilis* probably uses a computationally simple strategy to initiate landing and to control leg extension by relying primarily on only two static visual cues. This offers an alternative to previous models of landing control where animals require a constant update with dynamic visual cues. This work contributes to exploring the diversity of strategies to control locomotor behaviours, which could be fruitful not only for behavioural scientists but also from the perspective of bio-inspired technologies.

Paper III

Exploring the diversity of eyes is crucial for understanding how different animals use vision to interact with their environment. To date, comparative studies of eye anatomy are scarce because they often involve time-consuming or inefficient methods. X-ray micro-tomography (micro-CT) is a promising high-throughput imaging technique that enables the 3D anatomy of eyes to be reconstructed, but powerful tools are needed to perform fast conversions of these anatomical reconstructions into functional eye models. Thanks to an interdisciplinary collaboration between sensory biologists and computer scientists, chapter three addresses this methodological gap. My co-authors and myself developed a new computing method named *InSegtCone* that automatically segments the crystalline cones – an essential optical component – in the apposition compound eyes of arthropods. In this chapter, we describe the full auto-segmentation process of *InSegtCone*, showcase its application to three different insect compound eyes and evaluate its performance. Because it greatly accelerates time-consuming labelling, *InSegtCone* sets the ground for high-throughput analyses that are required for understanding the diversity of eyes in a large number of arthropods. This work can also provide inspiration for new ways to analyse 3D repeated structures, which is relevant to any natural, material or computational scientist working with tomographic images.

Paper IV

In this chapter, I used high-throughput micro-CT tools to quantify, compare and understand the diversity of visual traits of compound eyes in bumblebees. I found that the visual systems of bumblebees were far from identical, with variations across sizes, castes and species. Closely related bumblebee species did not share particularly similar eye properties. Instead, resemblances of visual traits were better explained by species sharing a similar visual ecology. Indeed, the eye parameter – a metric that measures the relative investment of a compound eye into resolution or sensitivity – was lower in queens of social parasitic species than of non-parasitic species. Workers of species associated with forested habitat had distinct visual traits, including a higher eye parameter, than those of species living in open landscapes. These diverse visual traits likely confer selective advantages to bumblebees given the specific ecological pressures that they are exposed to. We thus propose that social parasitism and forest habitat are drivers of the diversification of compound eyes in bumblebees. This work underlines the tight link between ecological variables and the structure and function of compound eyes in bees. Given that the visual system of bees plays a key role in guiding many essential behaviours, this highlights the value of including visual properties in trait-based approaches to predict the sensitivity of bees to anthropogenic changes.

Ecology and evolution of bees

Why study bees

There is no need to be an experienced entomologist to be familiar with the buzzing flight of a bumblebee, or to know that honeybees provide us with delicious honey. Outside of these well-known species, however, the public is less familiar with the 25 000 species of bees or members of the clade Anthophila (Goulson, 2010). In contrast to other hymenopterans, such as wasps and ants who often invite themselves to our picnic table, bees forage exclusively from flowers, eating mostly pollen as larvae and nectar as adults (Michener, 2007). Bees radiated during the Cretaceous together with flowering plants and both groups are co-adapted (Danforth et al., 2006). Plants display signals, such as attractive colours, odours, shapes and nectar rewards, that increase sexual reproduction via effective pollination (the transfer of pollen 'from the anthers to the stigma of the same or a different flower' (Goulson, 2010)), whereas bees harbour morphological and behavioural adaptations (e.g. pollen baskets, specialised mouthparts, colour preferences, foraging strategies) that make them effective discoverers and consumers of floral products (Patiny, 2012). Once collected, these products are carried back to the nest, bees are thus so-called 'central place foragers' that commute between their home and a foraging place. Insect pollinators, and especially bees (Willmer, 2011), play a key role in many ecosystems by pollinating about 80% of all flowering plant species (Ollerton et al., 2011), but this function is under threat as bee numbers have declined over the past decades. Pesticide use, habitat loss, invasive species and diseases are the main causes of this worrying decline (Brown and Paxton, 2009; Dicks et al., 2020) that could negatively impact many cultivated (Klein et al., 2007) and wild plants (Fontaine et al., 2005).

Despite their commonalities, bee species vary greatly in their ecology. You may encounter them in nearly all terrestrial biomes: savannas, tropical rainforests, alpine grasslands, agricultural landscapes and deserts, where they construct their nests that range from hexagonal arrays of wax to a single hole in mud (Michener, 2007). Each bee species typically visits a range of flower species, leading to a complex network of interdependence with plants. The width of a species' flower spectrum can vary dramatically, from oligolectic bees feeding on one to a handful of plant species, to polylectic bees that are foraging generalists (Goulson, 2010; Michener, 2007). Bees also vary in their degree of sociality. Most bees are solitary: a female lays eggs and raises her offspring on her own. At the other end of the spectrum, honeybees, bumblebees and stingless bees are eusocial. Eusociality is characterised by a division of labour between one or a few queens that lay eggs, and workers that forage, defend the hive, feed their mother's offspring, etc. Many species have intermediate levels of sociality, such as the chocolate mining bee *Andrena scotica* who can share the same nest with conspecifics without a division of labour. As in humans, in bees too, there is no game without cheaters. Inquinilism is a widespread strategy of social parasitism whereby the cheater bee exploits the services of other bees without contribution in return (Lhomme, 2009). Several bee taxa, such as cuckoo bumblebees, have evolved obligate social parasitism, and entirely depend on their host species to rear their offspring.

Their diversity makes bees ideal models for answering fundamental questions in ecology and evolutionary biology regarding sociality, foraging strategies, mutualism and senses. From a practical point of view, bees have a relatively well-resolved phylogeny and a wide behavioural repertoire (Chittka, 2017). Bees are also good models for understanding sensory biology and the neural basis of behaviour due to their small brains (in comparison to vertebrates) and their readiness to repeat foraging trips between a food source and their nest, which makes them easy to train. Finally (and perhaps most importantly) the little-explored biology of bees needs to be investigated further in order to develop efficient strategies for preserving them and their crucial contribution to the pollination of plants.

Bumblebees

Bumblebees (tribe: Bombini, family: Apidae) are eusocial bees that emerged about 30 million years ago in the Himalayan mountains and then dispersed to most continents (Hines, 2008). There are about 250 species of bumblebee (Goulson, 2010) that, in spite of being closely related (they are within the same genus *Bombus*) and performing very similar behaviours, live in extremely different biomes ***(Figure 1)***, ranging from cluttered tropical forests (e.g. *Bombus transversalis*) to featureless tundras (e.g. *Bombus monticola*) or deserts (e.g. *Bombus sonorus*). Bumblebees typically have an annual lifecycle: in spring, a queen emerges from hibernation in search for a suitable home, such as an abandoned rodent burrow or bird nest (Goulson, 2010). The queen initially forages intensely to feed the first workers that, once they are in sufficient numbers (from a handful up to several hundreds), take over most of her duties. At the end of the season, the colony begins to produce sexually capable males and/or females (gynes) that will mate outside the hive. Bumblebees are big, hairy insects usually tolerant to cold and adverse weather and capable of buzz pollination (gathering pollen by shaking the anthers), making them excellent pollinators (often better than honeybees (Willmer et al., 1994)), particularly in northern latitudes (Goulson, 2010). Unfortunately, they have undergone an alarming decline over the past decades, and the trend is likely to accelerate because of climate change (Rasmont et al., 2015; Sirois-Delisle and Kerr, 2018).

Figure 1. Diversity of bumblebee habitats. *Bombus transversalis (a)* lives in the lowland tropical rainforest, while *Bombus monticola (b)* thrives in the treeless tundra and *Bombus sonorus (c)* inhabits the Sonoran desert. *(a)* copyright John Asher / www.discoverlife.org. *(b)* copyright Malcolm Storey / www.discoverlife.org. *(c)* copyright John Asher / www.discoverlife.org.

Stingless bees

Stingless bees (tribe: Meliponini, family: Apidae) are tropical bees that appeared more than 60 million years ago (Michener and Grimaldi, 2006), probably in the southern hemisphere (Rasmussen and Cameron, 2007). All 500 species are eusocial with colonies of a few hundreds to over 10 000 workers (Wille, 1983). Workers construct a nest whose entrance differs in shape and size between species (Couvillon et al., 2008). Stingless bees have developed elaborate strategies to defend the hive against robbers and predators. For example, bees guard the hive entrance and inspect potential threats (Kelber and Zeil, 1990), harass identified intruders (Shackleton et al., 2015), recruit new defenders using alarm pheromones (Nunes et al., 2014) and obstruct the hive entrance in case of danger (Nunes et al., 2014). Stingless bees are crucial for the pollination of many tropical plant species, including crops such as mango, guava and tropical nuts (Heard, 1999).

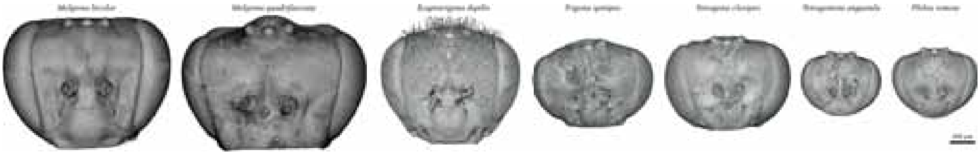


Figure 2. Size variability across species of stingless bees. X-ray microtomographic (micro-CT) images of stingless bee (tribe: Meliponini) heads. Each image is a volume rendering (orthographic view) of the scaled dried head of a female worker. Note that the antennae and mandibles were removed in all individuals, and the hair was only left in *Scaptotrigona depilis*.

Stingless bees differ in many aspects of their biology and ecology ***(Figure 2)***, including body size (Streinzer et al., 2016), activity period (Streinzer et al., 2016), visual ability (Duell, 2018; Streinzer et al., 2016), flight performance in relation to temperature (Duell, 2018) and nest defensiveness (Shackleton, 2018). In particular, the species-specific size and shape of the hive entrance may be tuned to a particular trade-off of foraging needs and defensiveness (Couvillon et al., 2008). For instance, a large hive entrance enables high traffic rates of returning and leaving foragers but requires substantial defence mechanisms. The first chapter of my thesis reveals that in *Scaptotrigona depilis* ***(Figure 3)***, returning workers accelerate just before touchdown on the hive entrance (Paper I, Tichit et al., 2020a) instead of decelerating as most animals (including other bees) do (Lee et al., 1993; Reber et al., 2016b; Srinivasan et al., 2000; van Breugel and Dickinson, 2012). A model of bee traffic suggests that this behaviour of 'accelerated landing' reduces the risk of traffic congestion (Tichit et al., 2020a). Thus, the ecological trade-off between foraging and defensiveness may have not only selected for nest construction behaviours but also for specific flight behaviours. My work adds to the body of knowledge showing that landing strategies in insects are far from universal (Baird et al., 2013) but instead depend on the ecological and behavioural context (Balebail et al., 2019; Chang et al., 2016; De Vries et al., 2020; Shackleton et al., 2019; Smith et al., 2020; Tichit et al., 2020a).

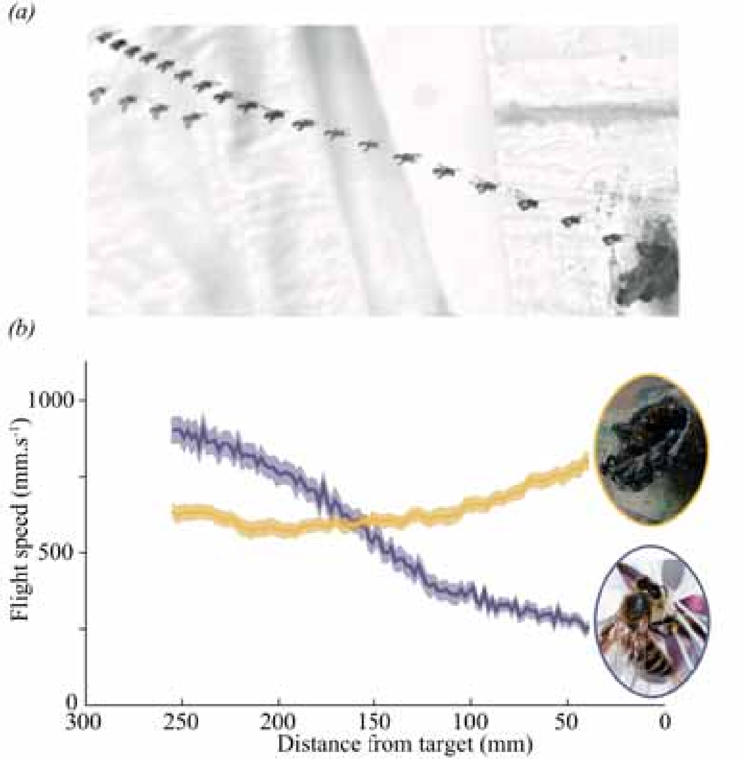
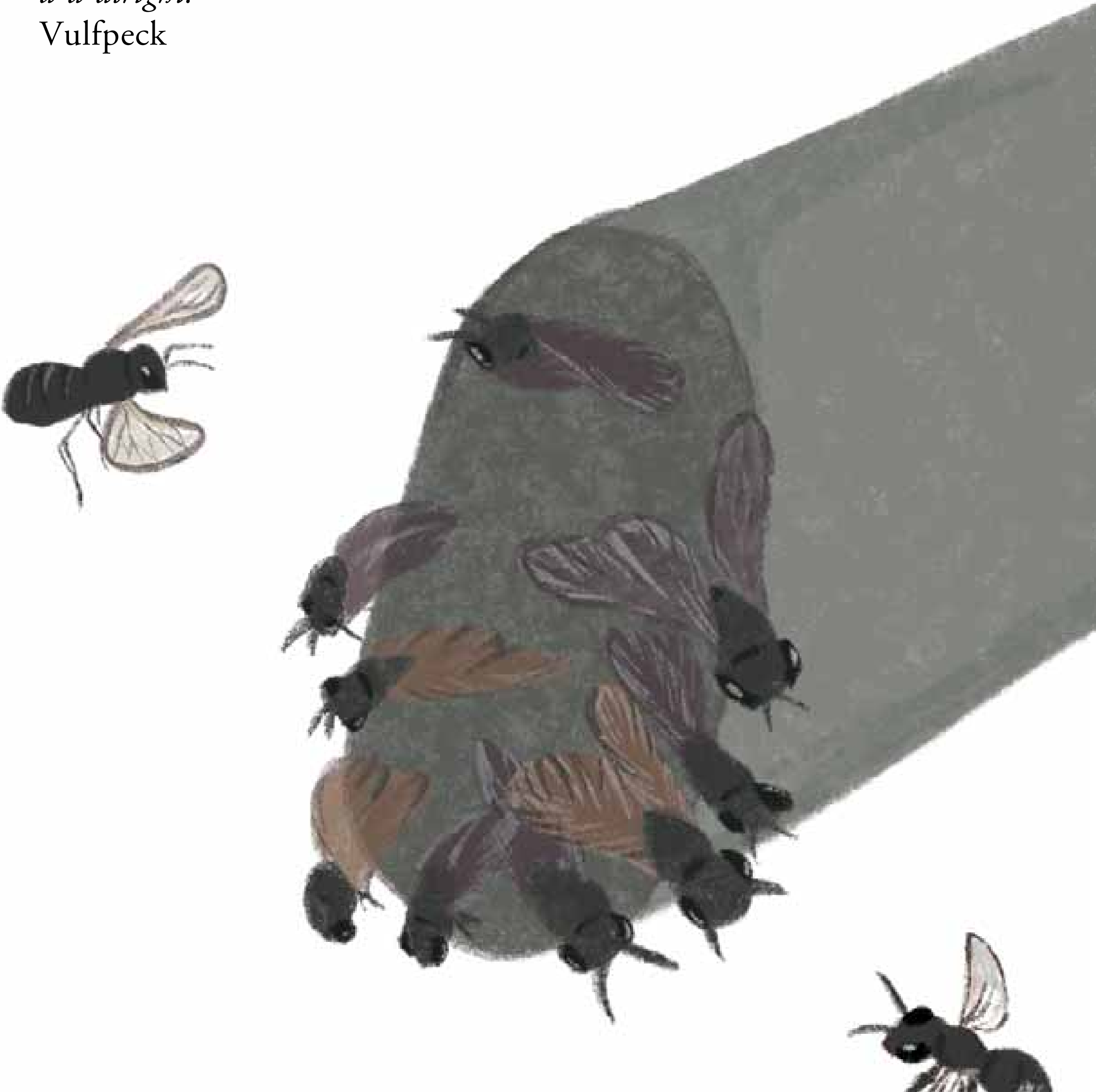


Figure 3: Accelerated landings in the stingless bee *Scaptotrigona depilis*. *(a)* Superimposed frames (resampled to 30 frames.s^{-1}) showing a typical landing sequence of *S. depilis* on the hive entrance (Tichit et al., 2020a). *(b)* The speed of *S. depilis* (orange) and *Apis mellifera* (purple) as they land on the hive entrance or a food source, respectively (adapted from Baird et al., 2020). The original data for *A. mellifera* (n = 26, Baird et al., 2013) and *S. depilis* (n = 52, Tichit et al., 2020) was interpolated for each flight at 2 mm intervals and then averaged. The shaded area represents the standard error of the mean. Picture credits: Emily Baird (*A. mellifera*) and Sheina Koffler (*S. depilis*).

“Open your wings and start to fly,
it’s a beautiful day to be alive,
a-a-alright!”
Vulfpeck



Commonality and diversity of visually-guided behaviours in bees

Why study bee vision

Senses, including vision, provide the main interface between an animal and its environment. Visual systems gather information about the environment, such as the location of a floral food source. This information is processed in the brain and provides the basis for a behaviour: a bee lands on a flower. Behaviours have consequences on the type of information that an animal can perceive in the environment at subsequent times (for example, the completion of a landing behaviour until touchdown will allow a bee to detect mechanical cues around its feet). The ability to use vision to control behaviours allows an animal to optimise its chances of successfully interacting with the environment whilst minimising the risks and energy costs, and thus provides fitness benefits by increasing its survival and/or number of offspring (Cronin et al., 2014). Visually guided behaviours have evolved through time and have been tuned by the selection pressures associated with the ecology of each species.

Bees rely heavily on vision for most behaviours, including controlling their flight, navigating, foraging and finding mates (Kelber and Somanathan, 2019). Investigating the visually-guided behaviours of bees thus allows us to understand how they interact with their environment across space and time. Visually-guided behaviour in bees is mediated by two types of eyes: three camera-type eyes called ocelli and a pair of apposition compound eyes that will be described in more detail in the section 'Commonality and diversity of bee eyes in relation to visual environment'.

Historically, the study of bee vision has been disproportionately focused on a few model species, such as the Western honeybee *Apis mellifera* and the Buff-tailed bumblebee *Bombus terrestris* (Chittka, 2017), leaving the visual abilities of most bee species largely unknown. In the present work, I started shifting this focus by investigating the diversity of the visual systems and behaviours of a range of bee species.

Studying bee vision can have useful 'side effects' in other fields of biology. For cognitive scientists, knowing the sensory basis of bee behaviour is essential for developing controlled experiments with informative results about the neural processes underlying it. For landscape or community ecologists, knowing the visual basis of bee behaviour enables an understanding of how they interact with the environment, such as in insect-plant pollination models (Ishii et al., 2019). Evolutionary biologists could examine the evolution of visual systems by exploring how they change across bee species with different phylogenetic relationships and ecological backgrounds. Finally, conservation biologists could explore if and how visual traits contribute to the vulnerability of bee species to environmental changes (Madliger, 2012) and elaborate sensory-based mitigation strategies (Horváth et al., 2010).

Flight control

Commuting flights

Box 1 motion cues

Flying insects rely extensively on visual cues generated by their own movement – or image motion cues – to control behaviours ***(Figure 4)***. To illustrate this, let us take a point at a distance D (m) and a bearing θ (deg) from a bee flying at a linear speed V (m.s^{-1}). This situation generates a pattern of motion on the bee's retina, or optic flow (OF). The translational component of OF can be described by its angular velocity $d\theta/dt$ (deg.s^{-1}) (Srinivasan, 2011):

$$d\theta/dt = \frac{\mathrm{V}\sin\theta}{D} \qquad (1)$$

Nearby objects will generate a greater magnitude of translational OF than those further away. This is a property of the interaction between the animal and the world that is very useful for the control of flight in many animals (e.g. Bhagavatula et al. 2011; Eckles, Roubik, and Nieh 2012), including bees (e.g. Srinivasan, 2011). Bumblebees (*Bombus terrestris*) can measure OF flexibly across their field of view (Linander et al., 2016, 2015). Note that when motion cues are generated through specifically dedicated movements, e.g. during learning flights, the term motion parallax is more appropriate (Horridge, 1986; Lehrer et al., 1988).

Flight is a risky enterprise, as crashing into obstacles could be harmful or cost energy (Mountcastle and Combes, 2014). Despite their small brain, bees are first-class pilots, which they achieve nearly exclusively using visual motion cues (Srinivasan, 2011). To fly efficiently and safely, bees need to control both their position in space and their flight speed.

To control their position in space, bees increase their distance to obstacles in the frontal field of view that generate greater magnitudes of OF (*Bombus terrestris*: Lecoeur et al., 2018; Linander et al., 2016; *Apis mellifera*: Srinivasan, 2011). When the distance to objects on both sides is very small, for example, when flying through narrow corridors, the honeybee *A. mellifera* (Srinivasan et al., 1991), the bumblebees *B. terrestris* and *B. impatiens* (Baird and Dacke, 2012; Dyhr and Higgins, 2010) and the nocturnal sweat bee *Megalopta genalis* (Baird et al., 2011) perform centring behaviours – they maintain an equal distance to each wall by balancing the lateral OF experienced in each compound eye. This behavioural response appears to be flexible and to vary between species. When the width of the corridor increases, *B. terrestris* prefer to rely instead on ventral OF from the ground (Linander et al., 2016), while *A. mellifera* start to follow one of the walls (Serres et al., 2008). However, when the distance between obstacles becomes very narrow, *B. terrestris* perform side-to-side flights to visually assess the aperture using OF contrast (Ravi et al., 2020, 2019), whereas the orchid bee *Euglossa imperialis* uses the brightness gradient, flying always toward the brightest and thereby safest point (Baird and Dacke, 2016). Finally, to regulate their vertical distance from the ground, bees may use OF cues in the ventral field of view (*Melipona panamica*: Eckles et al., 2012; *A. mellifera*: Portelli et al., 2010), which they (*A. mellifera*) might enhance using regular side-to-side oscillations during forward flight (Baird et al., 2021).

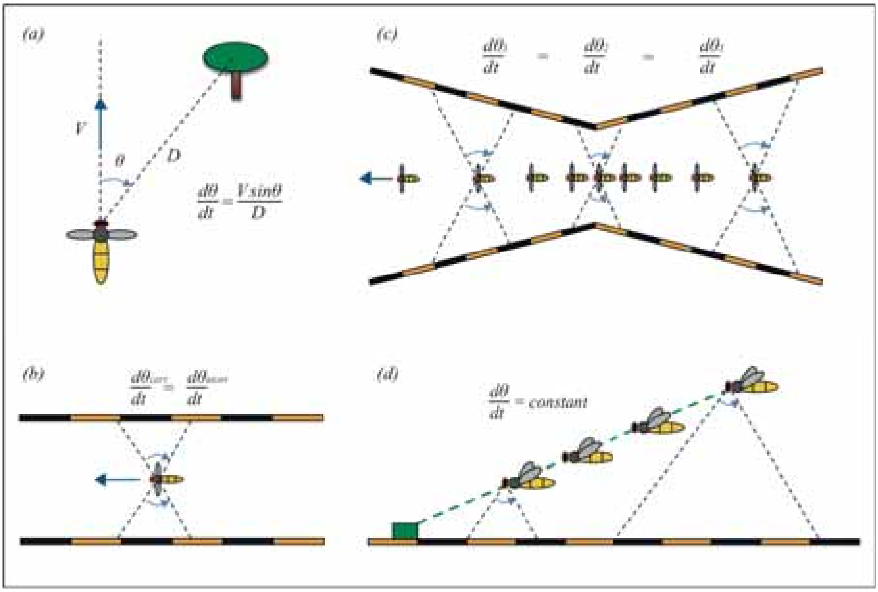


Figure 4: Bees use optic flow to control flight. *(a)* Definition of angular velocity (equation 1). *(b)* Bees that fly through a narrow gap balance the optic flow (OF) generated by their two eyes. *(c)* Regulation of flight speed by maintaining a constant OF. *(d)* Decrease of landing speed by maintaining a constant OF. Adapted from Srinivasan (2011).

Effectively avoiding collisions requires the ability to regulate the distance to nearby surfaces but also to control the speed of flight. Regulating flight speed gives the animal the chance to enact avoidance manoeuvres around obstacles whilst minimising the time spent on commuting. To do so, bees (*A. mellifera* and *B. terrestris*) hold the magnitude of translational OF constant through time (Baird et al., 2010, 2005), something they do regardless of other factors such as wind (*A. mellifera:* Baird et al., 2021; Barron, 2006). A consequence of this strategy is that flight speed will be reduced when the proximity of nearby obstacles, and thus the risk of collision, increases (Baird et al., 2005; Linander et al., 2016).

Little is known about how different bees control their trajectory and speed during commuting flights in different visual environments, but it is clear that all species do not 'fly the same' in identical circumstances (Baird et al., 2020). For example, there appear to be large disparities in the behavioural strategy for negotiating gaps in *E. imperialis* and *B. terrestris* (Baird and Dacke, 2016; Ravi et al., 2019). There are also fundamental differences in the control of trajectory and speed across honeybees (*A. mellifera* and *A. cerana*: Chakravarthi et al., 2018), bumblebees (*B. terrestris* and *B. impatiens*: Dyhr and Higgins, 2010; Linander et al., 2016) and sweat bees (*M. genalis*: Baird et al., 2011).

Landing

When landing on a target, bees must simultaneously coordinate their speed and trajectory towards the goal before extending their legs to make a safe touchdown. Here, again, bees make extensive use of motion cues. Honeybees (*Apis mellifera*) smoothly reduce their approach speed down to a safe value by keeping constant the angular rate of expansion $d\theta^T/dt$ of a vertical (Baird et al., 2013) or horizontal target (Srinivasan et al., 2000). The bumblebee *Bombus terrestris* (Reber et al., 2016b, 2016a) and sweat bee *Megalopta genalis* (Baird et al., 2015), that also decelerate before touchdown, presumably use the same strategy, whereas other animals maintain a constant ratio of $d\theta^T/dt$ relative to the angular size of the target θ^T (Lee et al., 1993; van Breugel and Dickinson, 2012). Like flies (Balebail et al., 2019; Tammero and Dickinson, 2002; Wagner, 1982), it is hypothesised that honeybees (*A. mellifera*) initiate landing when $d\theta^T/dt$ (absolute or relative to θ^T) reaches a certain threshold (Srinivasan et al., 2000). Finally, bees (*A. mellifera*, *B. terrestris*, *M. genalis*) extend their legs just prior to contact, a reflex that is thought to be triggered by motion or instantaneous cues, such as a threshold of θ^T (Baird et al., 2015; Evangelista et al., 2010; Reber et al., 2016a).

The course of a landing varies depending on external factors such as the orientation (Balebail et al., 2019; Liu et al., 2019) or visual properties (Caro et al., 2019) of the target, and internal factors such as differences between species. To support these diverse landing sequences, the underlying control mechanisms are likely to vary too. I explored the diversity of landing control mechanisms by investigating how the bee *Scaptotrigona depilis* control their unusual strategy of 'accelerated landings' before touching down on the hive entrance (paper II, Tichit et al., 2020b). *S. depilis* do not appear to use motion cues to control landing. Instead landing and leg extension are initiated when the angular size of the target θ^T reaches set thresholds. Interestingly, this simple control mechanism seems sufficient to coordinate smooth accelerated landings.

All this – still mostly unexplored – behavioural diversity of landing and commuting flight control could relate to differences in eye anatomy that, in turn, could be linked to differences in evolutionary history or to habitat-specific visual adaptations (Baird et al., 2020).

Navigation

Most bees are central place foragers that rely on their navigation abilities to identify and keep routes from a flower patch to their nest and vice versa (Mandal, 2018). Foraging honeybees (*Apis mellifera*), orchid bees (*Euplusia surinamensis*) and bumblebees (*Bombus hyperboreus*) may navigate five, ten or even twenty kilometres away from their hive (Beekman and Ratnieks, 2000; Janzen et al., 1971; Stenström and Bergman, 1998). Bees likely rely most heavily on vision to navigate (Mandal, 2018), although honeybees may also use irregularities of the earth's magnetic field (Frier et al., 1996; Walker and Bitterman, 1989) or olfactory cues as navigational landmarks (Menzel and Greggers, 2013) and to localise their hive (Saleh et al., 2007). By combining the knowledge about distance and directions over a trip, bees (*A. mellifera*) can use path integration to continuously calculate the shortest straight path for their return journey (Mandal, 2018). To estimate the distance travelled between their nest and a food source, honeybees and the stingless bees *Melipona seminigra* and *M. panamica* compute the distance travelled between two points using an odometer that integrates the OF experienced during flight (Eckles et al., 2012; Hrncir et al., 2003; Shafir and Barron, 2010).

To know the direction flown, honeybees (*A. mellifera*) use the sun as a navigational cue (Frisch, 1967) and can adjust their estimate as it changes position throughout the day (Lindauer, 1971). When clouds or foliage hide the sun, they can use instead the pattern of polarised light to infer its position in the sky (Kraft et al., 2011). The compass strategy of honeybees is common in other navigating animals (Dacke et al., 2014; Perez et al., 1997; Phillips and Waldvogel, 1988) and is likely to be similar in many bee species, although we currently know little about this.

In addition to using celestial cues to navigate, honeybees can rely on close-by or distant landmarks (Anderson, 1977), snapshots of a panorama (Cheng, 2000; Mandal, 2018) or the position of the skyline (Towne et al., 2017) to locate a desired goal. To memorise landmarks, bees typically perform learning or orientation flights, flying along arcs of rising altitude and radius away from a relevant position such as a food patch (Zeil et al., 1996). These learning flights seem to vary across size, sex and species. For example, small and large workers of *B. terrestris* perform orientation flights of different duration (Frasnelli et al., 2020), while males do so at flowers but not when leaving the nest

(Robert et al., 2017). Interestingly, when presented with a new landmark (a standing researcher), certain bumblebee species perform orientation flights while others do not (Goulson et al., 2004). During a field expedition in Northern Sweden, I confirmed this observation and extended the dataset to include boreal species of bumblebees by performing a similar experiment where I was standing near bees as a landmark *(**Figure 5**)*. It is possible, though unproven, that these interspecific differences in landmark learning relate to factors such as the difficulty of the homing task. This speculation is supported by the well-documented observation that different bees species travel different foraging distances (Crowther et al., 2019; Greenleaf, 1974; Redhead et al., 2016; Westphal et al., 2006). Additionally, social parasitic bumblebees with reduced navigational requirements never perform orientation flights (Goulson et al., 2004).

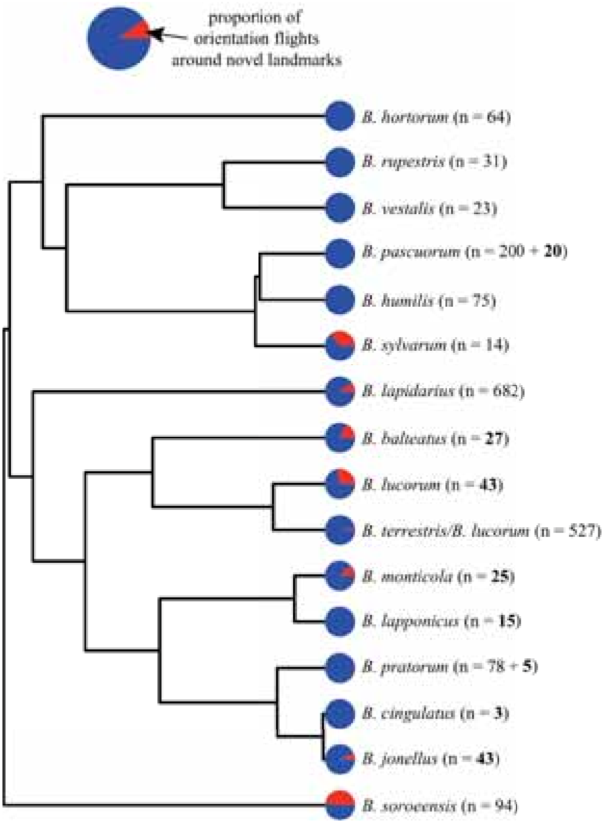


Figure 5: Interspecific diversity of orientation flights of bumblebees when presented with a novel landmark. The pie chart indicates the proportion of workers and queens that performed an orientation flight towards a researcher standing near them (red) or that continued foraging without any orientation behaviour (blue). Data was obtained from Goulson et al. (2004) and collected by Julia Meneghello and I near the research station in Abisko, Sweden (2019). The numbers of individuals tested in the previous study and/or by myself (in bold) are given in parenthesis. The results were mapped onto a previously published bumblebee phylogeny (Hines, 2008).

Finally, if bees get lost, they start a systematic search by making loops around their initial position to find familiar landmarks that can be used to guide them (Reynolds et al., 2007).

Foraging

Bees combine several behaviours during foraging: search flights, flower detection, flower choice, flower handling, feeding and departure (Sprayberry, 2018). Visual information plays an important role in most of these foraging activities ***(Figure 6)***, either alone or in combination with other senses such as olfaction.

Figure 6: Bees foraging on flowers. *(a)* Worker of *Tetragonula iridipennis* (credits: Gifty Alin Jacob). *(b)* Queen of *Bombus balteatus* (credits: Julia Meneghello).

Given the limited visual acuity of bees and the relatively small size of flowers, flower detection from a distance can only rely on few salient visual signals (Sprayberry, 2018) or on the combined signal generated by several flowers (Hempel de Ibarra et al., 2015). To detect a flower, honeybees (*Apis mellifera*) rely on its green contrast against the background (Dafni et al., 2007). These bees also detect and respond to conspicuous flower shapes or possibly movements caused by the wind (Dafni et al., 2007; Warren and James, 2008; Wolf, 1933).

Once a bee is close to a flower, a myriad of visual features are available to make a choice. As many flowers may provide poor nectar or pollen rewards, flower discrimination is important for a foraging bee (Raine et al., 2006). In the lab, bees can be trained to discriminate between two visual stimuli that differ with respect to size (Horridge et al., 1992), shape (Lehrer et al., 1995), symmetry (Giurfa et al., 2002), colour (Wehner, 2011), degree of polarisation (Foster et al., 2014), colour iridescence (Lunau, 2016) or the presence of a feeding conspecific (Kawaguchi et al., 2007). However, as there is a trade-off between choosing accurately and the time taken to discriminate (Chittka et al., 2003), bees may often use only a subset of all visual cues available for flower discrimination (Chittka and Raine, 2006), especially if the cost of errors is very low (for instance, if flowers are densely packed and easy to handle).

Bees have diverse visual foraging abilities that likely reflect differences in diets and habitat constraints (Dafni and Kevan, 1995). The honeybee *A. mellifera*, the bumblebee *Bombus terrestris* (Dyer et al., 2008), and the stingless bees *Tetragonula carbonaria* (Dyer et al., 2016) and *T. iridipennis* (Jezeera et al., in prep) differ in their colour discrimination and detection abilities, possibly reflecting differences in the habitats where they evolved (Dyer et al., 2008). In terms of innate colour preference, there are differences among bumblebee species (Raine et al., 2006) and even within bumblebee populations (Chittka et al., 2004) that could be linked to the range of flower species that they forage on. Moreover, unlike honeybees (*A. mellifera*), bumblebees (*B. terrestris*) seem to spontaneously prefer vertical flowers with bilateral symmetry over horizontal axial symmetry, which could be an adaptation to the types of flowers they feed on (Giurfa et al., 2002; Rodriguez et al., 2004; Wignall et al., 2006). In terms of flower constancy (the degree to which an individual limits its visits to a single flower species), some bumblebee species – such as *B. terrestris* – are more flower constant than others, e.g. *B. lapidarius* (Raine et al., 2006). All these differences are likely to be mirrored by variations in the morphology and physiology of the visual systems of these species (Dafni and Kevan, 1995).

Mating

There is a considerable diversity of mating strategies between bee species and sometimes even between populations (Paxton, 2005), with studies typically focussing on male behaviour (Alcock et al., 1978; Paxton, 2005). Unlike females, males are typically short-lived and invest most of their time and energy on maximising their mating success. One strategy is to wait directly inside or in front of a hive in an attempt to mate with emerging queens (Michener, 2007; Paxton et al., 1996). Another strategy is to search for queens by patrolling ***(Figure 7)*** between different nests, flower patches, or across a landscape (Paxton, 2005; Svensson, 1979). In the latter case, the probability of encountering a receptive female is very low, such that males often repeatedly mark objects at given sites along their route with a species-specific scent that attracts females (Kubo et al., 2017). Although this behaviour is, to a large extent, guided by olfaction, vision likely plays an important role in identifying suitable marking sites and returning to them (Awram, 1970), as well as detecting and approaching receptive queens (Free, 1971). A third male mating strategy is called perching, whereby males perch at a high site and start chasing any object that look like a flying queen. To do this, males need good eyes to detect and chase their small moving target (Gonzalez-Bellido et al., 2016; Ruttner, 1976). This behaviour is widespread among bees (Somanathan et al., 2017), though apparently uncommon in bumblebees (Schremmer, 1972; Streinzer and Spaethe, 2014). Here again, the different approaches to mating between sexes and species likely are associated with visual specialisations.

Figure 7: Patrolling male of *Bombus jonellus* landing on a queen dummy. Superimposed frames (resampled eight times to 15 frames.s^{-1}) showing the approach and landing trajectory (red) on a queen dummy (white arrow). The queen dummy was a black and orange ball (diameter ≈ 20 mm) hanging at a marking site along a patrolled route. I performed the experiment with the help of Julia Meneghello near the research station in Abisko, Sweden (2019).

"Jag ser inte en kott I den här skogen!"
Skånska humlepatrullen

Commonality and diversity of bee eyes in relation to the visual environment

Why and how to study and compare bee eyes

Visual systems have a high energetic cost (Niven and Laughlin, 2008), putting eyes under strong selective pressures to sample only the most relevant subset of the visual world (Cronin et al., 2014; Wehner, 1987), especially in invertebrates such as bees that have small brains in comparison to vertebrates. Because distinct behaviours require different sensory information and because the visual world varies widely in the availability and distribution of visual information, eyes have diversified in relation to the ecological needs specific to an animal, thus becoming 'matched filters' (Wehner, 1987). As a consequence, we cannot understand the diversity of visually guided behaviours in bees without exploring the corresponding variability of their visual systems.

Under the 'matched filter' hypothesis, a visual property has evolved as an adaptation that matches an ecologically relevant informational content (Snyder et al., 1977; Wehner, 1987). However, differences in visual traits may also arise without direct natural selection through other drivers such as phenotypic plasticity (Jones et al., 2013), genetic drift and chance (Chittka et al., 2004), pleiotropy (the side-effect of the evolution of another correlated trait) and exaptation (the result of a trait historically evolved under other pressures). To disentangle the adaptive hypothesis from other causes of eye diversification, investigating the diversity of bee eyes and visual behaviour requires an evolutionary perspective (Dangles et al., 2009; Gould and Lewontin, 1979; Raine et al., 2006). One way to do this is to perform comparative analyses of eye variability at different levels: between species (eg. in arthropod eyes: Farnier et al., 2015; Feller et al., 2020; Keesey et al., 2020; Scales and Butler, 2016; Streinzer and Spaethe, 2014a), populations (Perl and Niven, 2016a), individuals (Taylor et al., 2019) or life-stages (Evans and Fernald, 1990), and to integrate these into phylogenetic models (Chittka and Briscoe, 2001). Visual traits that have emerged several times in distant taxa are likely to be adaptations to similar ecological constraints.

How to quantify vision

Visual properties

To describe a digital screen, one may give its resolution in pixels. Similarly, for eyes, spatial resolution (hereafter referred to as resolution) is the smallest resolvable angle (or highest spatial frequency ν_s) subtended 'at the eye by two stripes in a grating of equal light and dark stripes' (Land, 1997). Spatial resolution is a crucial parameter of vision because it will determine the ability of an animal to see and interact with fine features, e.g. a food source (e.g. Dyer, Streinzer, and Garcia 2016) or a conspecific (e.g. Sheehan, Jinn, and Tibbetts 2014). In addition to resolution in space, animals need resolution in time to be able to detect changes in the visual world. Temporal resolution describes the sampling rate of the eye and limits an animal's ability to discern successive changes in visual stimuli. It is biologically relevant as it determines at what speed a moving object generates motion blur. To be able to see in a dim environment, eyes require a given optical sensitivity that describes the ability of the visual system to capture light (Warrant, 1999). In addition, spectral sensitivity reflects the capacity of an eye to differentiate different wavelengths of light, which provides the neural input for colour perception (Cronin et al., 2014). Similarly, the sensitivity of an eye to polarised light reveals if an animal is capable of using polarisation cues naturally present in visual scenes (Cronin et al., 2014) to guide behaviours such as navigation (Wehner, 2014). Finally, animals rarely sample from the whole visual world but instead concentrate sampling efforts on a restricted field of view. Measuring the extent and the shape of the field of view indicates which parts of the visual world are most informative to the animal (Cronin et al., 2014).

…must be traded-off

All eye properties cannot be maximised simultaneously. For instance, decreasing the smallest resolvable angle of the eye improves spatial resolution, but at the same time, this decreases sensitivity by reducing the area over which photons are captured. A longer duration of light capture enhances sensitivity but comes at the cost of temporal resolution. Consequently, visual parameters are, and must be, tuned according to the ecological needs of an animal, i.e. the range of light conditions, behavioural tasks and retinal speeds that a given portion of the eye is exposed to (Snyder et al., 1977). To compromise this, visual parameters are often tuned topologically across the eye (Cronin et al., 2014), such that different regions are optimised for specific ecologically-relevant information and behavioural tasks (e.g. in crabs and bees: Smolka and Hemmi, 2009; Taylor et al., 2019). We humans are familiar with this eye regionalisation, as our fovea achieves high resolving power over a small part of the visual field, while our peripheral vision samples a much larger region at a lower resolution.

Structure and function of the ocelli

Bees have three small eyes called ocelli *(**Figure 8**)*, typically positioned in a triangle arrangement on the top of the head (Michener, 2007). An ocellus is a camera-type eye: light passes through a single lens into the vitreous body and reaches photoreceptors (the light-receptive units) that form a cup-shaped retina (Land and Nilsson 2012). Typical insect ocelli have a curved, wide lens and a thick retina that provides high sensitivity and a large field of view (Mizunami, 1994; Warrant and McIntyre, 1993). However, in a recent study of the ocelli of the bumblebee *Bombus terrestris* (Wilby et al., 2019), we discovered that tufts of hair between and above the ocelli substantially reduce the field of view of each ocellus, although whether this is functional remains unclear. The structure of the photoreceptors of the ocelli in several bee species, including *Apis mellifera*, *B. terrestris*, *Amegilla asserta* and *Euglossa imperialis* suggests that they may be polarisation sensitive (Ribi et al., 2011; Ribi and Zeil, 2017; Taylor et al., 2015). The photoreceptors of bee ocelli also seem to be sensitive in the UV and green (Goldsmith and Ruck, 1958). Little is known about the temporal resolution of the ocellar photoreceptors of bees, but the large diameter of the second-order neurons likely have fast reaction times, as they do in other insects (Mizunami, 1994; Wilson, 1978). The properties of the ocelli – large visual field, high sensitivity, fast response time – are generally achieved at the cost of a poor spatial resolution (Ribi et al., 2011; Warrant et al., 2006).

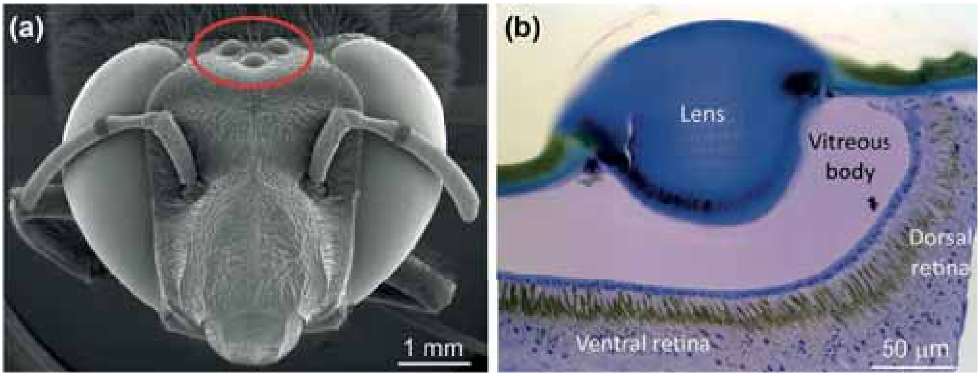


Figure 8: The ocelli of Euglossa imperialis (male). (a) Scanning electron micrograph of the head (Adapted from Taylor et al. 2015). (b) Sagittal section of the median ocellus (light microscopy). Adapted from Ribi and Zeil (2017).

Several non-mutually exclusive functions have been suggested for bee ocelli. As suggested in the locust (Wilson, 1978), the first role could be to stabilize head and body orientation in flight by regulating the relative amount of dark ground and bright sky within the ocellar fields of view. This theory is supported by behavioural evidence in non-hymenopteran insects such as locusts (Taylor, 1981), dragonflies (Stange, 1981) and blowflies (Parsons et al., 2006). The second function could be to provide celestial cues, e.g. polarisation cues, to guide compass-based navigation. A previous study on free-flying and walking *B. terricola* provided some behavioural indication that bees use the ocelli to steer according to polarized light at low light intensities (Wellington, 1974).

Structure and function of the apposition compound eyes

Bees have a pair of apposition compound eyes ***(Figure 9)*** with many optical units called ommatidia (Land, 1997). There are varying numbers of ommatidia: I found, for example, less than 3000 in the small *Tetragonula iridipennis* (Jezeera et al., in prep), but more than 11 000 in the large *Xylocopa tenuiscapa* (paper IV). Each ommatidium consists of a crystalline cone covered by a cuticular corneal lens – forming a (usually) hexagonal facet visible on the eye surface – that focuses light onto the distal tip of a single photoreceptor. Each photoreceptor is made of eight retinular cells surrounded by pigment cells that prevent light from passing to neighbouring units. Retinular cells are fused in a central microvillous region to form a light-sensitive rhabdom where light is coded into a neural signal that is sent to the optic lobe (Ribi et al., 2008). Light propagates through the whole rhabdom, meaning that an ommatidium averages the intensity of all light it receives, acting as a single sampling unit. Wavelength information (interpreted as colour) is detected by the relative output of three different types of retinular cell with specific spectral sensitivities that peak in the UV, blue and green (Autrum and Zwehl, 1964; Meyer-Rochow, 1980). Bees are thus trichromats (Frisch, 1914).

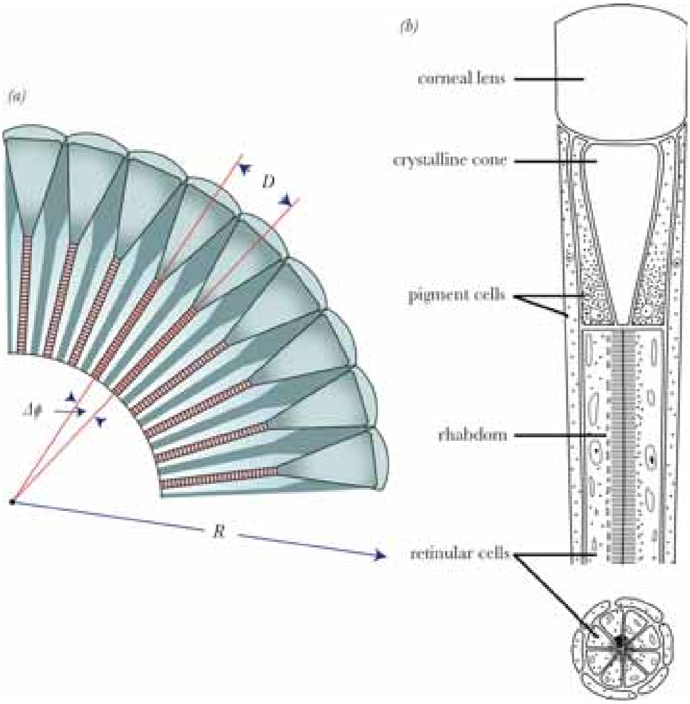


Figure 9: Building blocks of a bee compound eye. A compound eye *(a)* is made of a juxtaposition of ommatidia *(b)* whose angular spacing $\Delta\phi$ is the ultimate determinant of spatial resolution. Adapted from Cronin et al. (2014).

In compound eyes, the angle between two adjacent ommatidia $\Delta\phi$ is called the interommatidial angle (IO angle):

$$\Delta\phi = \frac{D}{R} \tag{2}$$

Where D is the diameter of the corneal facet and R the local radius of curvature of the eye. The IO angle is a meaningful parameter that reflects spatial resolution by indicating the local density of ommatidia (a small IO angle gives a potential for high spatial resolution). However, spatial resolution is more accurately expressed by the acceptance angle $\Delta\rho$ that encompasses the effects of the quality of the optics, the retina and of motion blur (Land, 1997; Snyder, 1979):

$$\Delta\rho = \sqrt{{\Delta\rho_a}^2 + {\Delta\rho_b}^2 + {\Delta\rho_c}^2} \approx \sqrt{\left(K\frac{d}{f}e^{\frac{1}{V}}\right)^2 + \left(\frac{\lambda}{D}\right)^2 + (v\Delta t)^2} \tag{3}$$

$\Delta\rho_a$ reflects the effect of rhabdom width d, that is *(1)* finite, which sets a geometrical limit to resolution, and *(2)* small (Aepli et al., 1985), such that only one or two waveguide modes of light propagate into the rhabdom and other modes are lost (Warrant and McIntyre, 1993). f, V and K represent respectively the focal length, the V-number describing the number and shapes of propagated light modes, and a constant value. $\Delta\rho_b$ corresponds to the blurring caused by the diffraction of light of wavelength λ through a lens of diameter D, which is critical in bee compound eyes given the small lens diameters (Warrant and McIntyre 1993). $\Delta\rho_c$ represents motion blur with Δt the integration time of the rhabdom and υ the angular velocity across the retina.

In the case of a broad spectrum extended scene, the optical sensitivity of a compound eye is (Land, 1997):

$$S = \left(\frac{\pi}{4}\right)^2 D^2 \Delta\rho^2 \frac{kl}{2.3+kl} \qquad (4)$$

Where D is the facet diameter, l and k the length, and absorption coefficient, and $\Delta\rho$ the acceptance angle of the rhabdoms, respectively (Cronin et al., 2014).

Resolution and sensitivity are traded-off according to the type of information that is most crucial to a bee in a specific eye region (Land, 1997; Snyder et al., 1977). To explore the relative investment in these two visual capacities, a useful metric is the eye parameter p – the product of facet diameter and IO angle:

$$p = D\Delta\phi \qquad (5)$$

When an eye region is limited by diffraction only, the cut-off frequency ν_{co} is determined by the spacing of ommatidia such that:

$$\nu_{co} = \frac{1}{2\Delta\phi} = \frac{\lambda}{D} \qquad (6)$$

A value of the eye parameter tending toward 0.29 µm.rad indicates a diffraction-limited region that maximises spatial resolution. Conversely, an eye parameter above 1 µm.rad suggests an investment towards improved sensitivity (Snyder, 1979). Interestingly, previous studies reported a minimum eye parameter around 0.5 µm.rad in diurnal bees and flies (Snyder et al., 1977; Somanathan et al., 2017), while I have measured mean eye parameters ranging from 0.7 µm.rad to 0.8 µm.rad across bumblebee species (paper IV). Even though these insects are active in daylight, they have a range of relatively high eye parameters that probably correspond to an adaptation to the high motion blur generated by their own flight (Land and Nilsson, 2012; Snyder et al., 1977).

The combination of the viewing directions of all ommatidia across the eye determines its field of view. In honeybees (*Apis mellifera*), the field of view of the two eyes is nearly spherical (Seidl and Kaiser, 1981) and presents a dorso-ventral region of binocular overlap similar to the one found in bumblebees whose function is still unclear as it is very unlikely to be used for stereopsis (Taylor et al., 2019).

Box 2 micro-CT for optical modelling 1/2

Most previous studies have reduced the anatomical complexity of the compound eyes by performing 2D measurements on different portions of the eye, such as measuring eye area from images (Scales and Butler, 2016), facet diameters from flattened eye replicas (Streinzer et al., 2013), or rhabdom width from local sections (Warrant and McIntyre, 1991). When 3D measurements were taken, this was usually done on a restricted portion of the field of view, such as with the pseudopupil method that measures IO angles (Rutowski et al., 2009).

However, bee eyes are complex 3D objects that require a good technique capable of extracting high-quality anatomical data in order to reconstruct accurate optical models. During my thesis, I developed a new method with relatively high-throughput using X-ray microtomography (micro-CT) of insect eyes (Taylor et al., 2019, 2015; Wilby et al., 2019). By preserving the 3D structure of the eye, this method enables us to describe vision in world-referenced coordinates and to make comparisons between individuals or species.

To perform high-throughput, high resolution scans with micro-CT, we need an X-ray source with high energy, such as the one generated at a synchrotron (in our case Diamond light source in Oxfordshire, UK (Peić et al., 2013; Rau et al., 2011)). During scanning, a parallel coherent (the beam is straight and all rays are in phase with each other) polychromatic beam is shot at a sample and is absorbed differently because of changes in density or composition of the material. After being converted to visible light with a scintillator and being focussed through a microscope lens, a detailed absorption image of the structure – sometimes with sub-micrometre resolution – is formed (Taylor et al., 2015). The contrast in this image is often enhanced by staining the specimen with an X-ray absorbing heavy metal (osmium tetroxide in our case). By rotating the sample on the stage by a few tenths of a degree between each image (typically 2000/4000 images over 180 deg), we can record the entire sample in 3D. These images are then converted to image stacks via a complex reconstruction algorithm (Baird and Taylor, 2017).

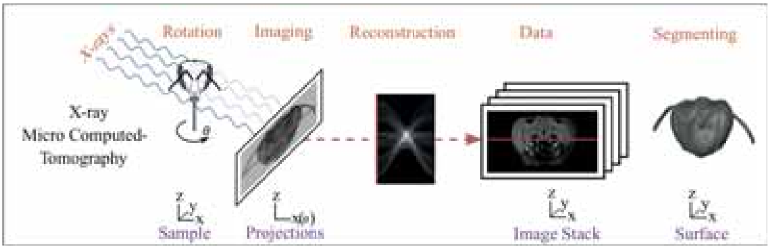


Figure 10: Imaging, reconstruction and processing of samples with micro-CT. Adapted from Baird and Taylor (2017).

Bees also possess a region at the dorsal limit of the eye, called the dorsal rim area (Aepli et al., 1985; Labhart and Meyer, 1999), with a few ommatidia whose structure differs from a general ommatidium: *(1)* each ommatidium contains nine and not eight retinular cells, *(2)* the rhabdoms are wider, *(3)* the microvilli of a photoreceptor point in two orthogonal directions, making it sensitive to a specific e-vector of polarised light.

While the insect dorsal rim area is specialised for the detection of polarised light (Aepli et al., 1985; Labhart and Meyer, 1999), Compound eyes as a whole, and apposition compound eyes in particular, are well suited for high resolution, motion and colour vision in bright light (Warrant and McIntyre, 1993). Bees utilise their compound eyes for tasks that require the perception of form and colour, including the perception of single objects (e.g. a landmark, a flower, another bee) and patterns of motion, such as the visual landscape passing by the eye or the looming image of an approaching obstacle (Avarguès-Weber et al., 2012).

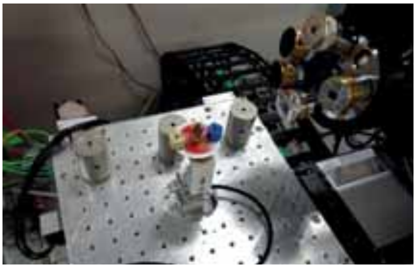
Box 2 micro-CT for optical modelling 2/2

From the image stacks generated from the tomographic scans, we extract relevant input for optical study with the 3D visualisation and analysis software Amira (FEI). This step includes three main techniques:

- Measurement of relevant features: e.g. the shortest distance between the ocelli, or the lens diameters.
- Segmentation: this is the labelling of surfaces or volumes of interest, such as the layer of crystalline cones in the compound eye. While it can sometimes be performed automatically with the help of intensity-based thresholding, this step currently includes a large part of manual labelling.
- Registration: the alignment of structures relative to each other or to the world. For instance, the high-resolution scan of a compound eye can be registered on a low-resolution scan of a head that is itself aligned with respect to the world coordinates.

To approximate the field of view of a compound eye, we use the normals to the lens outer surface as indications of the viewing directions of the eye in space. On a high-resolution scan of a bee compound eye (voxel size = 1.6 µm), we segment the volumes of the lens, crystalline cones and retina, as well as their outer and inner surfaces. When the inner structures are not well-preserved or visible (for instance, in a dried specimen), we only label the lens surface. On the same scan, we measure the diameter of seven adjacent facets on at least twenty sampling points on the eye surface. We then register the labelled compound eye on a segmented bee head (voxel size = 4 µm typically), placed itself in a reference position relative to the world. These registered labels are imported to MATLAB (The Mathworks Inc., Natick, MA, USA) for optical analyses.

Facet shapes are interpolated across the eye using an inverse distance-weighted interpolant, thereby estimating the facet area. Equidistant sampling points are chosen on the eye, and normals onto the world are determined by locally fitting a quadratic polynomial at each sampling point to the local eye surface within a circular region of interest of fixed radius *r*. The angle between two normals from the centres of adjacent facets is the corneal IO angle (an approximation of the IO angle) and the local eye curvature is then calculated with equation 2. When the inner structures are preserved, we also calculate the thickness of the layers of cuticular lenses, crystalline cones and photoreceptors at the sampling points.



A moss carder bee is ready to be scanned with micro-CT at Diamond light source, UK (2019).

We independently calculate the number of facets by *(1)* dividing the eye area with the mean facet area, and *(2)* from the density of the projected normals on the eye surface. The above-described interpolation method is iterated over with a different radius *r* of the region of interest for normal determination until it reaches the optimal *r* that gives the best match between the two estimates of facet numbers. The topology of parameters is then interpolated across the field of view. Finally, the field of view of one eye is mirrored to obtain the field of view of the other eye and the region of binocular overlap.

Variations within an individual: topology of eye properties

Although some properties, including the distribution and spectral sensitivities of the three types of photoreceptors, remain relatively constant across bee species and genera (Lehrer, 1998), most parameters (light sensitivity, spatial and temporal resolution, etc.) vary topologically across bee eyes (Land, 1997). The study of the topology of visual properties gives us the possibility to identify investments into eye regions of behavioural or ecological importance. In insects, several types of regions are usually identified (Land, 1997; Land and Eckert, 1985). *(1)* Bright zones have wide facets but big IO angles, thus a high sensitivity and poor resolution. *(2)* Acute zones have wide facets and small IO angles (Horridge, 1978), achieving high sensitivity and resolution. This combination of high sensitivity and high resolution is only possible through a flattening of the eye that locally increases the radius of curvature. Finally, *(3)* a region with small IO angles but small facets only reaches high acuity in bright light. This region of the eye will from now on be referred to as an area of high-resolution.

In bees, there is no clear evidence of a bright zone, as reported in the male hoverfly *Eristalis tenax* (Straw et al., 2006), but acute zones are common. Male *Apis mellifera* have an acute zone that covers the entire dorsal hemisphere (Menzel et al., 1991), while males of some carpenter bees (*Xylocopa spp.*) have a dorso-frontal acute zone (Somanathan et al., 2017). Dorsal (respectively, centro-frontal) acute zones have been strongly suggested (but not fully demonstrated) in males of other honeybee species (Streinzer et al., 2013) and of perching bumblebees (Streinzer and Spaethe, 2014). These conspicuous acute zones in males are most likely adaptations to perching mating that requires detection and chasing of small dark targets (females).

In conjunction with regionalisation, visual parameters tend to change gradually across the compound eye ***(Figure 11)***. Facet diameter typically increases along a dorso-ventral gradient (Streinzer et al., 2013; Taylor et al., 2019), while the topology of IO angle is more complex (Somanathan et al., 2009; Taylor et al., 2019), with the horizontal and vertical components following distinct trends (Land, 1997). In other flying insects, such as butterflies (Rutowski et al., 2009), the horizontal IO angle typically increases along a fronto-lateral gradient and the vertical IO angle increases when departing from the equator. This is thought to be an adaptation that matches the pattern of motion blur generated by forward-flight and that would lead to a forward-facing area of high resolution with the smallest average IO angle (Land, 1997). This seems to be the case in female carpenter bees (Somanathan et al., 2009). In honeybees and bumblebees, however, the region with minimal IO angle seems to be instead spread vertically around the equator at an azimuth of about 40-60 deg (Baumgärtner, 1928; Taylor et al., 2019). This suggests that the topology of IO angle in these species may be related to constraints other than the ones due to motion blur, for instance, to detect relevant objects such as flowers and terrestrial landmarks located medio-laterally (Lehrer, 1998; Taylor et al., 2019).

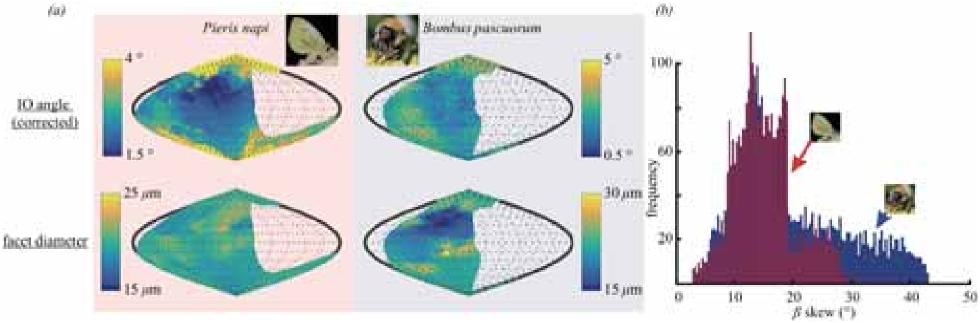


Figure 11: Visual properties vary topologically and across species. *(a)* Sinusoidal maps of IO angle and facet diameter on the field of view of the eye of the butterfly *Pieris napi* (female) and the bumblebee *Bombus pascuorum* (worker) scanned with micro-CT. Contrary to the corneal IO angle, the corrected IO angle accounts for the skewed viewing directions of the crystalline cones segmented with the tool *InSegtCone*. Note that both properties vary topologically across the field of view. For example, *P. napi* possesses a dorso-frontal acute zone with small IO angles and large facets. *(b)* Histograms of the ß skew between the viewing directions of crystalline cones and the normal axes to the corneal facets for both species. Note that the ß skew is typically larger in *B. pascuorum* than in *P. napi*. Picture credits: *P. napi* by Emily baird and *B. pascuorum* by Jerzystrzelecki - Own work, CC BY 3.0, https://commons.wikimedia.org/w/index.php?curid=25934860.

Analyses of the fields of view of ocelli suggest that they have areas of binocular (Wilby et al. 2019, *Bombus terrestris*) or even trinocular overlap (Taylor et al. 2015, *Euglossa imperialis*) and may be also regionalised. For instance, the retina of the ocelli of honeybees and bumblebees is bipartite: the ventral retina receives light from the sky, whereas the dorsal retina samples from the skyline (Ribi et al., 2011; Ribi and Zeil, 2018). This suggests a dual usage for flight stabilisation and celestial compass input.

While in principle, the viewing directions of the crystalline cones of compound eyes are mostly aligned with the normal axes to the corneal facets, ommatidia towards the border of the eye can have their viewing direction skewed (Baumgärtner, 1928), which could stretch the limits of the field of view beyond those predicted from the external anatomy. The topological variations of the ommatidial skew are still mostly unknown. To address this, I developed a computing method named *InSegtCone* to automatically segment the crystalline cones in apposition compound eyes scanned with micro-CT (paper III). This new tool will improve the accuracy of the field of view and resolution estimates by quantifying the visual IO angle instead of the corneal IO angle (Stavenga, 1979). Furthermore, I found that the topology of the ommatidial skew varied between insect groups *(**Figure 11**)*, suggesting that this parameter is more flexible across the eyes of bees (*B. pascuorum*) than of butterflies (*Pieris napi*).

Variations within a species: sex, caste and size

As mentioned above, the eyes of female bees often differ from those of male bees, particularly when the latter have conspicuous compound eye regionalisations linked to perching behaviour. Male honeybees, stingless bees and bumblebees also tend to have bigger ocelli (Ribi et al., 1989; Streinzer et al., 2013; Streinzer and Spaethe, 2014). In contrast to female workers, the ocelli of male *Apis mellifera* seemingly point forward, suggesting a unique role in skyline detection (Ribi et al., 2011). Honeybee queens, which spend most of their time inside the nest and do not forage, have relatively poor resolution but high sensitivity (few wide facets) in comparison to workers (Streinzer et al., 2013). In a recent study, I showed that the visual properties of compound eyes are influenced by caste in species of patrolling bumblebees (paper IV). Workers had typically the lowest values for eye size, facet number and diameter, queens had the highest values for eye size, facet number and diameter, and males had intermediate values. These relationships are consistent with previous comparisons in bumblebees (Streinzer and Spaethe, 2014).

Many bumblebee species, like *Bombus terrestris*, can vary tremendously in body size (Goulson, 2010; Loken, 1973) – even within a single hive, which has consequences for their visual capabilities. Large workers of *B. terrestris* have a wider field of view, more ommatidia (Taylor et al., 2019), smaller minimum IO angles and wider facets than small conspecifics which gives them better single object resolution (Spaethe, 2003). This is also the case in *B. lapidarius* and *B. pascuorum* where large workers fly under lower light intensities than small conspecifics (Kapustjanskij et al., 2007).

Box 3 allometry

Allometry refers to the study of how a trait scales with the size of an organism. Studying allometry is relevant because it indicates investment in a given trait in relation to available resources (Perl and Niven, 2016b). The relationship between a trait Y and a measure of body/organ size x is described by a power function:

$$Y = b.x^a \quad (7)$$

This provides two parameters: the scaling exponent a, and the initial growth index b (Huxley and Teissier, 1936). When the scaling exponent is equal, lower, or higher than one, there is isometry, negative allometry or positive allometry, respectively. The scaling exponent of eye size relative to body size is usually negative (Jander and Jander, 2002; Taylor et al., 2019), meaning that eye size increases more slowly than body size.

While smaller individuals generally have poorer vision than bigger ones, allometric studies may reveal the core of visual parameters that are essential to maintain an eye's performance. Furthermore, a comparison of allometric relationships between families (Jander and Jander, 2002), species (Makarova, Meyer-Rochow, and Polilov 2019) or populations (Perl and Niven, 2016a) can reveal a differential allocation of visual parameters**.** For example, in a colony of wood ants *Formica rufa*, facet numbers increased with body size, while the neighbouring colony invested primarily in wider facets (Perl and Niven, 2016a).

Variations between species: lifestyle and habitat

Most of the previous studies on interspecific diversity of bee eyes focused on the effect of size (Jander and Jander, 2002), activity period (i.e. if the bee is diurnal, crepuscular or nocturnal) (Warrant, 2008), or the interplay between the two (Streinzer et al., 2016). Adaptations to nocturnal or crepuscular lifestyles are well documented in the sweat bee *Megalopta genalis* (Warrant, 2008) and some carpenter bees (Somanathan et al., 2009), and suspected for the honeybee *Apis dorsata* (Streinzer et al., 2013) and the stingless bee *Trigonisca pipioli* (Streinzer et al., 2016). In these nocturnal and crepuscular bees, ocellar lenses are typically wide (Somanathan et al., 2009) with thick and densely packed photoreceptors (Warrant, 2008), while *Megalopta genalis* seem to sacrifice temporal resolution to increase photon catch (Berry et al., 2011). Compound eyes of bees active in dim-light are relatively larger, with wider facets and wider rhabdoms than their diurnal counterparts (Warrant, 2008).

What about subtler effects of ecological factors other than those of the activity period? There is some evidence that visual traits are associated with predatory lifestyle in beetles (Bauer and Kredler, 2011), with microhabitats in psyllids, fruit flies and damselflies (Farnier et al., 2015; Keesey et al., 2020; Scales and Butler, 2016) or with social interactions in wasps (Sheehan et al., 2014). In bees, however, the only published study providing some indication of this concerns the ocellar system of the orchid bee *Euglossa imperialis* (Taylor et al., 2015). In this species, the fields of view of each large ocellus overlap in a dorsal trinocular region that is probably sensitive to polarised light, whereas the monocular regions point laterally and receive a relatively focused image (***Figure 12***). These two areas might have evolved to fulfil different functions (celestial navigation, flight stabilisation, visual discrimination) in a challenging environment: a dense rainforest where the horizon is out of sight, and only small patches of the sky are visible (Taylor et al., 2015).

Figure 12. Model of the ocelli of *Euglossa imperialis* from micro-CT. The large ocelli of *E. imperialis* (male) are probably adapted for navigation and flight control in the dim and cluttered rainforest. Credits: Gavin Taylor.

To explore the effects of ecology and phylogeny on visual parameters in bee eyes, I used micro-CT tools to compare the visual properties of compound eyes across 27 species of bumblebees (paper IV). I found that the eye parameter was lower in queens of social parasitic species than of non-parasitic species. Moreover, workers of species associated with forested habitat had distinct visual properties, including a higher eye parameter, than species living in open landscapes. This study suggests for the first time that social parasitism and habitat drive the diversification of compound eyes in bumblebees.

“Cafard : contempler le vol
du bourdon me l’enlève.”
Sylvain Tesson

Conclusion, limitations, challenges and perspective

In this introduction to my doctoral thesis, I showed how diverse and interconnected the ecologies, visual behaviours, and eyes of bees are. This approach underlies the four chapters of my thesis. Chapter one lies at the interface between ecology and behaviour; chapter two investigates an interaction between behaviour and vision; chapter three focuses on visual anatomy; chapter four loops into the interplay between visual anatomy and ecology.

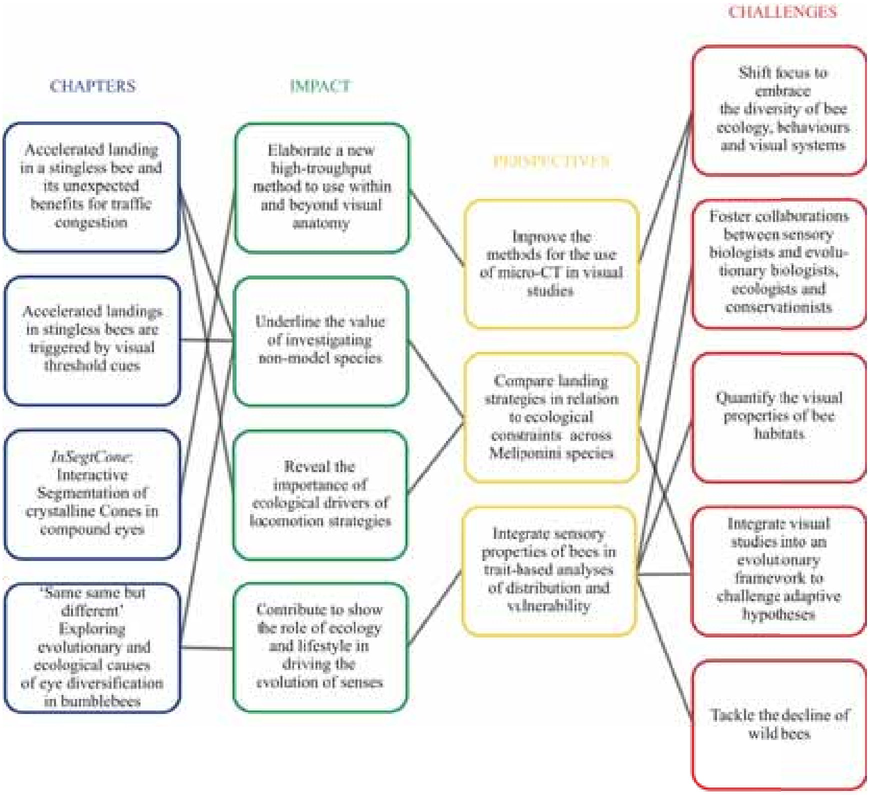


Figure 13: Impact, perspectives and future challenges of this thesis.

Abbreviations

IO angle: inter-ommatidial angle
Micro-CT: X-ray microtomography
OF: optic flow.

Collecting snacks during a field expedition near Manaus (Brazil) in 2016 with Cristiane Krug and Gavin Taylor.

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Acknowledgements

First of all, I would like to anticipate my fallible memory by thanking all the people whom I will forget to acknowledge in the following lines. Also, my apologies to readers for mixing languages. I will never do it again…promis juré!

Emily, I have learnt so much thanks to you and to your enthusiasm. Shortly after our first meetings, I realised how much of a supervising expert you are. Thank you for achieving this perfect equilibrium between support and autonomy, and for helping me to find the best in myself and others. Thanks also for not minding my obsession with trains, my skiing retreats, and my poor rapping skills!

Marie, Du har varit här och hjälpt mig från början. Jag är tacksam för att du ofta ställde dem viktiga frågorna som fick mig att tänka om min forskning. Tack också för att du introducerade mig till Biologishowen och gav mig spindelmansdräkten. Jag uppskattar mycket att du såg till att inkludera mig i dyngbaggegruppen, trots att mina djur rullar inte ett skit!

Dan, tack för att du har hållit koll på mig under den här resan. Vad skönt att du är en sån rolig och avslappnad chef som man inte skräms av att prata med! Keep up with the ‘Dan moment’ (whenever the next PhD party takes place), those are fun.

Christoffer, du har varit en mycket uppmärksam mentor. Tack för dem regelbundna samtalen vi har haft och som har hjälpt mig reflektera över min vetenskaplig upplevelse, livets betydelse… och var det serveras bästa lunchen!

Tack **Carina** och **Eva** för hjälpen med mina experiment och att ni svarade mina frågor. Att ni gör att syngruppen är livfull. Och att ni tände ljus i vårt mörka lunchrum, när natten var stor och stum.

Merci beaucoup **Ola G** för ditt stöd i labbet. Du är utan tvekan den duktigaste på franska i hela rummet B-224! Tack också till **Lars** för hjälpen i verkstaden, och till **Eric H** för de fina fika samtalen.

Jag är mycket tacksam till er tre: **Ylwa**, **Katarina** och **Sara B**. Tack för er tålamod trots alla mina försenade mejl och saknande formulär.

I am very grateful to all the past, present (and future?!) **Vision Group** members that I have met. Even "i min vildaste fantasi", I had not dreamt of a better work environment. You made me feel welcome from the very beginning. Thanks for that! A special hug to my friends from the third floor: **Marcel** Duchamp, Château **Kirwan**, **Josi** of the fried forest, **Atticus**azo, und **Andrea**… sogar!

Thanks to the **dung beetle group** for accepting me despite my weird animals. Tack **Yakir** for the winning advice you gave me more than once. **James**, you fostered my passion for statistics.

Lucky me for getting an adoptive lab and university in Stockholm on top of the originals! **Maxence**, **Zahra**, **Océane**, **Craig**, Vun Wen Jie alias **VJ**, **Marie G**, **Zanna** and **Ernesto**, you are great to work with, and fun, and kind, and…'no thank you'! I am also thankful to the **zootis members** for the fun times at Tovetorp and the support while sitting in my writing hermitage at SU.

Tack till Biologishowens team! På botten av Showenspyramiden finns jag, som skrattar med **Jacob**, som skojar med **Lina**, som dansar med **Julian**, som showar med **Lana**, och på toppen av pyramiden finns det en toppregissör, i det här fallet Doctor **Reber**!

During these four and a half years, I have had the chance to attend exciting conferences and to visit inspiring labs. I am grateful to them for welcoming me: the group of **Denis Michez** in Belgium, of **Lars Chittka** and of **Richard Gill** in the UK, the Brains on Boards network, as well as organisers of the ICIV, BLAM, ICTMS and SCAPE conferences. Thanks to **Eric Warrant**, **Per Lundberg**, **Charlie Cornwallis**, **Johan Ekroos**, **Jörgen Ripa** and **Anna Gårdmark** for organising mind-opening courses. Big up to the students of the sensory ecology, and the community ecology courses, we had good fun together.

A huge tack/thanks/merci/gracias to all my **collaborators and students** who helped me with my projects. I would not have made it without you! In particular, I am grateful to **Tunhe**, **Martin K**, **Vedrana** and **Anders Dahl**, as well as to the **Diamond team** in Oxfordshire: **Andrew**, **Kaz**, and all the night-shifters. **Viktor**, thanks for playing the Hangman game with me at four in the morning. **Inga**, Tack for being my friend and helping me with scanning despite my stu…dious face. **Gavin**, you have been a mentor, and I have learned a bunch from you. I hope that we will have a chance to meet one day over a couple of pamonhas! I am grateful to all the ones who supported me during my expeditions to Brazil. Agradecimentos especais to **Isa**, **Sheina**, **Rodolfo**, **Cacau**, **Elisa**, **Crisitiane** and obviamente **Carola**. I would also like to thank **Almut**, **Asmi**, **Hema** and her lab for an exciting collaborative project. **Statistics helpdesk**, what would the department be without you?! Thanks to the helpers and the staff at the **Abisko Research Station**. En particular, gracias a **Julia** por ser la asistente de campo mas requeté piola del mundo mundial!

In prevision of my PhD defence, I would like to thank the opponent **Martin How** and the members of the examining committee for accepting to take part in the final step of this adventure. Thanks also to **Maj Rundlöf** for being the opponent during my half-time examination.

Thanks to **Pilar**, **Johanna C**, **Peter**, **Cynthia**, **Kevin**, **Tomasz**, **Olesia**, **Jochen**, **Cara**, **Stanley**, **Tini**, **Mikael** for the shared picnics, BBQs, lundalopp and marvel-lous times.

I would not be here without the teachers and mentors who supported me during my early years as a baby biologist. Merci à ces professeurs qui m'ont fait grandir intellectuellement: **M. Hurni**, **M. Huet**, **Mme Blaise** et tant d'autres. Thanks to the researchers who supported me during my Master's projects: **Jasminca**, **Guy** and **Annemarie**.

I am so happy to have crossed the raging river that separated me from the ecology building. Thanks to the visitors and organisers of **Pub Einar**. Tack/thanks/merci/gracias/Danke to **Ann-Kathrin**, **Aivars**, **Ola O**, **Linus**, **Hélène**, **Romain**, **Ye**, **Mig(o)uel**, **Katrine**, **Qinyang**, **Maarit**, **Hanna S**, **Hanna L** , **Hanna B**, **Philip**, **Maria**, **Samantha**, **Pablo**, **Dániel**, **Elsa**, **Martin**, **Lulu**, **Carlota**, **Tristan**, **Johanna Y, Amanda, Utku, Gróa, Micaela**, **Albert/Carles**, **Humberto**, **Milda**, **Raphael** and **Ainara**. Thanks **Margarida**, **Weerachon**, **Xi**, **Beatriz**, **Juan Pablo** and **Oscar** for having invited me to some of the best PhD parties, back in the old times where most of the alcohol was not on people's hands. Thank you, **Katja** and **Carlos**, for accepting to be toastmasters for my PhD party (but not thank you, **virus** for most likely ruining it). Also, Thanks a lot, **Mai**, for illustrating my thesis.

During my PhD, I have spent a fair amount of time sitting in trains. Luckily, I found spontaneous **train companions** who taught me a bit of Chinese, helped me rehearse my flash talk and shared German doughnuts with me. I am grateful to **train companies** for making it possible, and to the **Schengen countries** for letting me travel through. Framför allt, tack **Sverige** för att ha adopterat mig under alla dessa år. Tack också till **Sara** från hårsalongen för att du var den första som pratade svenska med mig!

To my friends outside of academia, I am so lucky to know you all. Merci à **Féfé** et **Camcam** pour m'avoir initié à la fin-du-mondologie. Des bisous à **Albérique** et sa grandissante clique, à **Clara**, **Gilles**, **Marine** & **Svetli**, et **Carolin** & **Damina**; j'espère vous revoir tous bientôt. Merci aussi à **Raphaëlle**, **Estelle**, **Ana**, **Louis**, **Fanny**, **Pauline** & **Laurent**, **Alex**, et **Thomas P** pour les moments partagés lors de mes passages éclairs en France. Un abrazo a mis amigos "cubanos": **Cuau**, **Olaysi** y **Lore**. To **Theo H** and his family/friends: prøv-li-å-læs-her!

All my gratitude to the ones who came to explore Sweden with me: le ptit père **Simon**, les trois Morots (**Alicia**, **Myriam** et **Théo T**), **Irene**, le **gang des profs** de Vauvert, **Chouch** et son frère, **Audrey**, **Irène**, **Danielle** und der **David**.

It took some time, but I was lucky to find wonderful friends here in Sweden. Tack **Anders** för att du umgås med mig trots att jag fick N och inte S som andra bokstaven. Tack **Ellen** och vänner för att vi spelade musik tillsammans. Merci **Morgan** et **Erika** pour m'avoir nourri de cinéma et de crème fouettée. **Veronica**, me mostraste que la amistad es mas fuerte que los gatitos y perritos "pourritos". Tack medlemmar i **PUSH Sverige** för vår gemensam engagemang. Jag är så glad att ha dig som väninna **Alice**, förhoppningsvist kan vi göra en tågresa i Europa nån dag i framtiden. I am thankful to the housemates who successfully accepted to live with a weird French guy: **Lucas**, **Gabriel**, **Mary-Bell**, **Carlo**, **Christina**, **Suzanne**, **Thomas**, and in particular **Johanna**. Just one pancake from you and I know it's gonna be a lovely daaaaay.

Sitara, I will be cool and chill. But for some unknown reason, this last year of my PhD has been particularly nice. Weird – slash – I regret nothing!

Je ne serais pas devenu ce que je suis sans **ma famille**. Merci à mes grands-parents, mes oncles, mes tantes, mes cousins/cousines, parrain/marraine, et à tous les autres. **Papa**, **maman**, il m'est impossible de décrire en quelques lignes toutes les raisons pour lesquelles je vous dois tout. Si je ne devais dire qu'une chose en lien avec ce drôle de bouquin, c'est un immense merci pour avoir stimulé ma curiosité pour la nature depuis tout petit, pour ne pas vous être trop fâchés quand je nourrissais les fourmis avec mes corn flakes, et pour m'avoir soutenu tout au long de mes études. **Julie**, ma petite sœur préférée, tu m'as aussi soutenu et a influencé ma vie sans forcément t'en rendre compte : nous avons tous les deux grandi depuis dix-neuf ans !

Finally, **Bees**, you shall receive my infinite gratitude (especially the ones of you who were volunteered for my experiments)! Thanks also for not caring about my PhD thesis, or about the dubious choices that Humans make, and just bumbling about your life.

"Fake it till you make it!"

Printed by Media-Tryck, Lund 2021 NORDIC SWAN ECOLABEL 3041 0903

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Lund University
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ISBN 978-91-7895-785-9