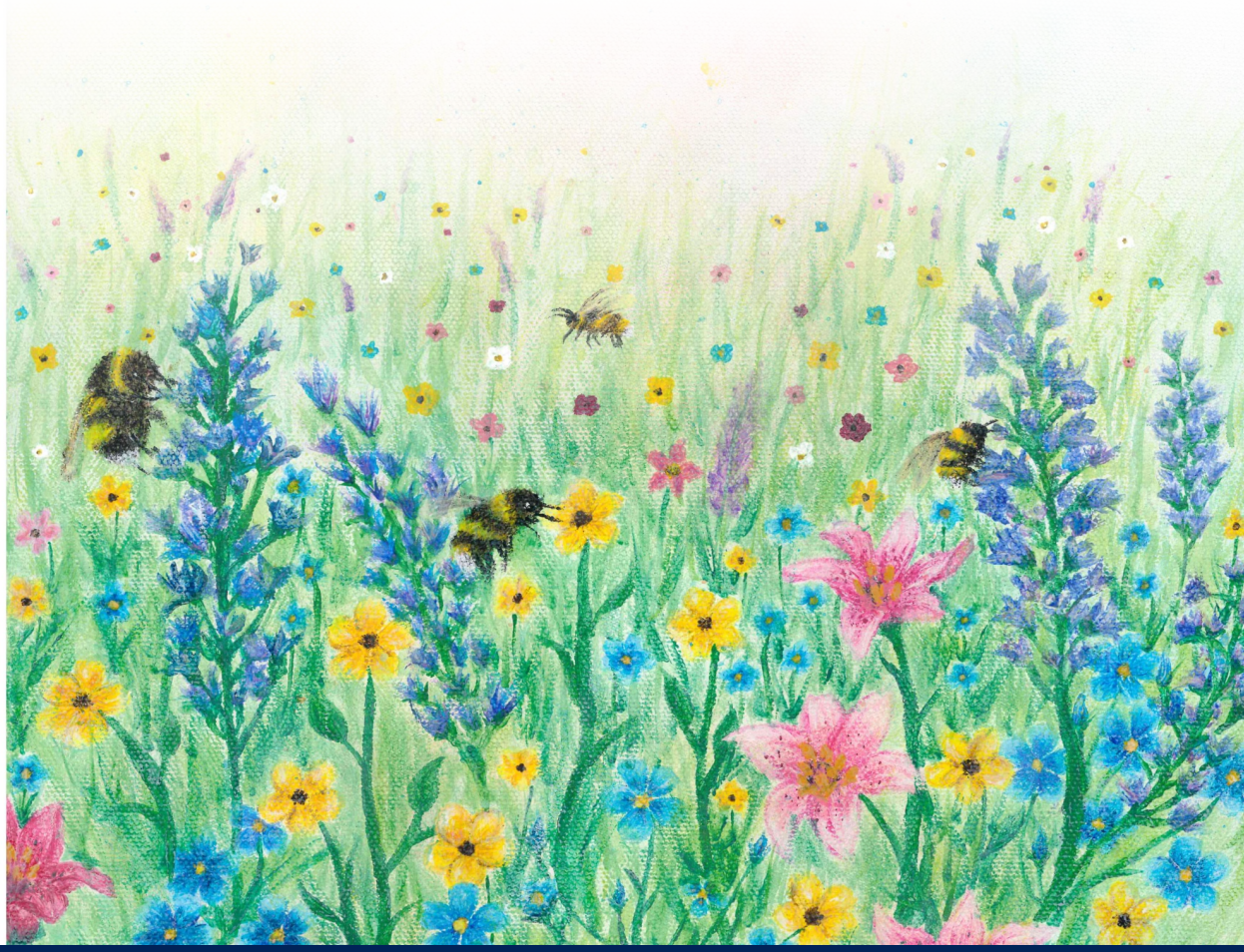
Stockholm University

# Understanding insect pollinator responses to climate change

Guadalupe Sepulveda



Doctoral Thesis in Functional Zoomorphology at Stockholm University, Sweden 2025

# Understanding insect pollinator responses to climate change


## Guadalupe Sepulveda



Academic dissertation for the Degree of Doctor of Philosophy in Functional Zoomorphology at Stockholm University to be publicly defended on Friday 12 September 2025 at 09.30 in Vivi Täckholmsalen (Q-salen), NPQ-huset, Svante Arrhenius väg 20.



### Abstract

Bumblebees (genus Bombus) are key pollinators in many ecosystems, yet their foraging performance and pollination efficiency are highly sensitive to environmental conditions, particularly temperature. As global temperatures undergo rapid changes due to climate change, understanding how thermal variation affects bumblebee behavior, physiology, and biomechanics is crucial for predicting potential disruptions to pollination services. Bumblebees possess a unique ability among insects to generate internal heat and are regarded as cold-adapted specialists. However, this adaptation also makes them highly vulnerable to rising environmental temperatures. Using a combination of laboratory experiments and field observations with commercial bumblebees, this thesis explores the impact of environmental temperature on bumblebee foraging behavior, flight control, vision, and pollination performance. In Chapter I, we examine how temperature impacts commercial bumblebee colonies by surveying foraging activity in a field site using both radio frequency identification (RFID) tags and manual surveys. We measured colony activity (number of departures and arrivals) as well as bumblebee body temperature upon depature and arrival and monitored colony and environmental temperature. Our results showed that while Biobest workers began foraging at cooler temperatures and increased both their foraging duration and pollen collection as environmental temperature rose, Koppert colonies exhibited relatively stable foraging behavior across temperatures, with shorter trips and less temperature-dependent pollen collection. These findings highlight the need to consider breeder-specific traits when choosing colonies for crop pollination in different climates. In Chapter II, we used laboratory experiments to understand how environmental temperature affects bumblebee body temperature and thermoregulation during different behaviors (i.e., during resting, pre-flight, and post-flight). We measured head, thorax, and abdomen temperature. We found that the effect of environmental temperature on bumblebee body temperature differs across behavioral contexts and that bumblebees use a counter-current heat exchanger to thermoregulate during during/ after flight. In Chapter III, we aimed to understand how increasing temperatures and decreasing light availability affect bumblebee visual performance and flight control. We measured visual performance by recording electroretinogram responses of bumblebees at different temperatures and light intensities. Additionally, by recording bumblebees flying during periods of dim and bright light at different temperatures, we assessed components of flight control, including flight speed, straightness, and centering. Photoreceptor SNR peaked at intermediate temperatures, declining at both low and high extremes. We found that bumblebees increase their flight speed as temperature increases, but only in bright light and this is aided by the increase in visual performance. On the contrary, during periods of dim light and lower temperatures, bumblebees fly slower likely caused by decrase in the visual performance. In Chapter IV, we examined how temperature influences the foraging behavior (i.e., number of flowers visited and time spent on each flower) of bumblebees using buzz-pollinated Solanum rostratum plants. We also investigated the vibratory mechanics of buzz pollination—a process in which bees generate rapid thoracic vibrations to extract pollen from flowers with poricidal anthers. We found that bumblebee foraging activity is affected by temperature, with bumblebees decreasing the amount of time spent on each flower and visiting more flowers per minute. This temperature-induced variation in behavior affected the reproductive outcome of the plants, with fewer fruits and seeds being produced by plants that were pollinated by bees at the higher temperature. We also found that vibration frequency, amplitude, and pollen release efficiency are significantly affected by temperature. By integrating ecology, behavior, physiology, and biomechanics, this thesis provides novel insights into the thermal sensitivity of bumblebees and their pollination effectiveness. The results emphasize the vulnerability of bumblebee populations and pollination services in a changing climate, underscoring the need for conservation strategies that promote pollinator resilience.



**Keywords:** *climate change, heatwaves, pollination, bees, physiology, behavior.*

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# Understanding insect pollinator responses to climate change

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I. **Sepúlveda-Rodríguez G**[†], Araújo P[†], de Assis S, Baird E. (2025). Insights into commercial bumblebee foraging dynamics (manuscript).

II. **Sepúlveda-Rodríguez G**, Roberts KT, Araújo P, Lehmann P, Baird E. (2024). Bumblebee thermoregulation at increasing temperatures is affected by behavioral state. *Journal of Thermal Biology*, *121*,103830. https://doi.org/10.1016/j.jtherbio.2024.103830

III. **Sepúlveda-Rodríguez G**, Ilić M, Škorjanc A, Araújo P, Belušič G, Baird E. (2025). Bumblebee flight control and vision are impacted by environmental temperature and light availability (manuscript).

IV. **Sepúlveda-Rodríguez G**, Araújo P, Gay L, Gérard M, Renner TA, Woodrow C, Baird E[‡], Vallejo-Marín M[‡]. (2025). Elevated air temperature impairs bumblebee pollination effectiveness and plant reproduction (manuscript).

[†]These authors contributed equally to this work and share first authorship

[‡]These authors contributed equally to this work and share senior authorship

Candidate contribution to thesis articles*

| | I | II | III | IV |
|---|---|---|---|---|
| Conceived the study | Substantial | Substantial | Substantial | Substantial |
| Designed the study | Substantial | Substantial | Substantial | Substantial |
| Collected the data | Substantial | Substantial | Substantial | Substantial |
| Analyzed the data | Substantial | Substantial | Substantial | Substantial |
| Manuscript preparation | Substantial | Substantial | Substantial | Substantial |

***Contribution explanation**
Minor: contributed in some way, but contribution was limited
Significant: provided a significant contribution to the work
Substantial: took the lead role and performed the majority of the work

I am also co-author of the following articles that were written during the course of my doctoral studies, but are not included in this thesis:

Woodrow C[†], **Sepúlveda-Rodríguez G**[†], Rajan S, Mitschke M. Baird E[‡], Vallejo-Marín M[‡]. (2025). Increasing temperatures affect thoracic muscle performance in Arctic bumblebees (manuscript).

Gérard M, Gardelin E, Lehmann P, Roberts KT, **Sepúlveda-Rodríguez G,** Sisquella C, Baird E. (2024). Experimental elevated temperature affects bumblebee foraging and flight speed. *Proceedings B*, *291*(2033), 20241598. https://doi.org/10.1098/rspb.2024.1598

[†]These authors contributed equally to this work and share first authorship

[‡]These authors contributed equally to this work and share senior authorship

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# Introduction

## *Insect pollinators and climate change*

The hum of insect wings has long been the soundtrack of thriving ecosystems. From wildflower meadows to vast agricultural fields, pollinators are nature's unseen workforce, maintaining the delicate balance of plant and animal life. Yet this crucial ecological relationship is being severely disrupted by accelerating climate change (Turner et al., 2020; Harvey et al., 2023). Rising temperatures, unpredictable seasons, and extreme weather events are reshaping the world that insects have adapted to over millions of years.

Insects form the backbone of terrestrial pollination networks, enabling the reproduction of nearly 90% of flowering plant species and contributing directly to global food security (Van der Sluijs & Vaage, 2016; Maggi et al., 2024). Their interactions with plants are finely tuned to local environmental conditions, including temperature, humidity, and phenology (Hegland et al., 2009). However, as climatic patterns shift, mismatches between insect activity and flowering times are becoming increasingly common (Gérard et al., 2020). These climatic disruptions threaten to decouple long-standing mutualisms, with cascading effects on ecosystem structure and function.

Moreover, climate change alters not just when and where insects operate, but how they function. Elevated temperatures can influence insect development (Gérard et al., 2022a), metabolic rates (Gérard et al., 2024), and flight performance (Kenna et al., 2021), while also exacerbating physiological stress. Heatwaves, droughts, and extreme precipitation events can reduce survival rates and disrupt foraging behaviors, ultimately diminishing pollination efficiency (Rosenberger, 2024). Insects already facing pressure from habitat loss (Wagner, 2020), pesticide exposure (Müller, 2018), and disease (Didham et al., 2020) are now navigating a rapidly changing climate that challenges their ecological roles.

## *Insect pollination and climate change*

Pollination involves the transfer of pollen from the male reproductive organs (anthers) of a flower to the female reproductive organs (stigma) of the same or another flower, leading to fertilization and the production of seeds (Frankel & Galun, 1977). Around 75% of crops consumed by humans rely on animal pollinators to increase quality and/or yield (Aizen et al., 2009; Fijen et al., 2018; Tong et al., 2023), with insects such as bees and butterflies being by far the largest and most successful group (Potts et al., 2016). Sensory input (vision and olfaction, for example), flight control (maneuverability, landing, and collision avoidance), and cognitive abilities (navigation, learning, and memory) are crucial for insects to perform these pollination services (Gérard et al., 2023). As insects have only a limited capacity to regulate their body temperature, these behavioral and physiological processes are affected by ambient temperature (Abram et al., 2017). Research has already shown a rapid decline in insect pollinator populations caused by climate change pressures, such as the increase of frequency and intensity of heatwaves and global average temperature (Halsch et al., 2021; Harvey et al., 2023). Nonetheless, very little research has focused on quantifying the direct effect of temperature changes (average or heatwaves) on insect pollinator physiology and foraging behavior, although understanding this is crucial for identifying and predicting the effect of forthcoming temperature changes on the ecosystem services they provide.

Among the most vital pollinators are bees, small but powerful architects of biodiversity (Patel et al., 2021). Within this group, bumblebees, with their distinctive buzz and remarkable cold-weather resilience, play an especially crucial role in temperate ecosystems (Parrey et al., 2022). But even these hardy insects are not immune to change. As temperatures rise, their physiology, sensory abilities, and behavior are being pushed to new limits, with potential consequences for the plants and ecosystems that depend on them (Maebe et al., 2021).

This thesis explores how temperature affects bumblebee physiology, sensing, and behavior, shedding light on the intricate ways climate shapes the lives of these essential pollinators. By understanding these relationships, we can better grasp the challenges insect

pollinators will face in a warming world and what their fate might mean for the future of ecosystems and food production alike.

# Bumblebees

## *What is a bumblebee?*

Bumblebees are members of the genus *Bombus* within the family Apidae, order Hymenoptera, comprising over 250 extant species distributed primarily across temperate regions of the Northern Hemisphere, with some representatives in South America (Hines, 2008). Phylogenetically, bumblebees are closely related to the stingless bees (tribe Meliponini), and their evolutionary success is attributed to their generalist foraging strategies, high mobility, and adaptability to diverse habitats (Goulson, 2003).

Bumblebees are eusocial insects characterized by their robust, hairy bodies, bright warning colors, and the presence of a corbicula, also known as a pollen basket, on the hind legs of females (Goulson, 2003). Their colonies are typically annual, founded by a single fertilized queen that has survived the winter, and organized into a caste system consisting of reproductive queens, sterile female workers, and males (Röseler & Van Honk, 1990). To support this life cycle, especially in cooler climates, bumblebees possess a key physiological adaptation: the ability to generate heat internally (Heinrich, 1993). They can decouple their wings from their indirect flight muscles, allowing these muscles to contract rapidly without wing movement – a process known as shivering thermogenesis (Heinrich, 1993). This generates metabolic heat in the thorax, enabling bumblebees to warm their flight muscles before takeoff and to maintain elevated body temperatures during foraging, even in low ambient temperatures or cloudy conditions (Corbet et al., 1993; Heinrich, 1993).

This same ability to decouple the wings from the flight muscles is also used during buzz pollination (sonication), a foraging behavior in which bumblebees vibrate flowers to release pollen from poricidal anthers (Vallejo-Marín, 2022). Bumblebees are among a subset genera in the Apidae family capable of performing buzz pollination, which involves gripping the flower and rapidly contracting their flight muscles to produce powerful vibrations that dislodge pollen inaccessible to many other pollinators (Pritchard & Vallejo-Marín, 2020). This

dual use of muscle decoupling—for both thermoregulation and pollen extraction—makes bumblebees particularly effective and versatile pollinators of wild flora and a variety of agricultural crops.

## *Lifecycle of a bumblebee*

The lifecycle of bumblebees (*Bombus* spp.) in Northern Europe is closely aligned with the temperate, highly seasonal climate characteristics of the region (Rasmont et al., 2015). Most species are univoltine, completing their life cycle within a single year (Gurel et al., 2008), although shifts in climatic patterns could promote some species to become bivoltine or multivoltine (Potapov et al., 2017). The cycle begins in early spring, typically between March and May, depending on local temperature regimes and elevation. Overwintered queens that have survived the diapause period in protected, insulated microhabitats, such as leaf litter, disused rodent burrows, or beneath tree roots, emerge as ambient temperatures consistently rise above freezing. These queens are mated from the previous year's season and must rapidly replenish depleted fat reserves by foraging on early-flowering plants. They search for suitable nesting sites, which vary by species but commonly include underground cavities, tussocks of grass, or abandoned mammal nests (Heinrich, 2004).

Once a nest site is selected, the queen constructs wax cells and provisions them with pollen and nectar to support the development of her first brood. The initial eggs, laid soon after nest establishment, develop into female workers. During this stage, the queen performs all colony tasks, including foraging, nest maintenance, and thermoregulation of the brood, which she accomplishes through shivering thermogenesis (Goulson, 2003; Heinrich, 2004). After approximately 3 - 4 weeks, the first cohort of workers emerges. These workers gradually assume responsibility for foraging and brood care, enabling the queen to specialize in egg-laying. Throughout late spring and early summer, the colony grows rapidly in size, with some species reaching several hundred individuals at peak development.

By mid- to late summer, as floral resources begin to decline and colony size plateaus, the queen alters her reproductive strategy and begins producing both haploid (unfertilized) and diploid (fertilized) eggs, giving rise to males and gynes (future queens, referred to here as princesses), respectively (Martinet et al., 2023). Males typically leave the nest shortly after

eclosion and do not return, spending their remaining days seeking princesses to mate with and feeding opportunistically (typically only on nectar) (Belsky et al., 2020). After mating, males die and newly-mated princesses (now referred to as queens) disperse in search of overwintering habitats, where they will enter diapause triggered by declining photoperiod and temperature cues (Heinrich, 2004). The original colony, including the founding queen and all remaining workers, undergoes senescence and collapses as temperatures drop and floral resources become scarce in late summer or early autumn. Thus, the entire cycle is renewed solely through the survival of the queens. This seasonal lifecycle is finely tuned to environmental conditions in Northern Europe and plays a critical role in the phenological synchronization between bumblebee colony dynamics and the availability of floral resources (Goulson, 2003).

## *Bumblebees as a study system*

Amongst all insect pollinators, bumblebees (genus *Bombus*) play a significant role in the areas they inhabit (Plath, 1925). As key pollinators of many flowering plants, bumblebees help maintain biodiversity and support global food production (Goulson et al., 2008) – for many crops, bumblebees are 2 - 4 times more effective pollinators than honeybees and solitary bees (Willmer et al., 1994; Goodell & Thomson, 1996; Estay et al., 2001; Thomson & Goodell, 2001). Bumblebees exhibit remarkable thermoregulatory abilities that allow them to thrive in various environmental conditions; they have physiological, behavioral, and morphological characteristics that enable them to forage and pollinate in conditions that are suboptimal for other insects (Heinrich, 2005; Pimsler et al., 2020). For example, bumblebees have exceptional vision during periods of low light (i.e., during dawn and dusk) (Meyer-Rochow, 2019) and the cold adaptations of many species (Hines, 2008), such as large body sizes and dense fur, allow them to fly in very low temperatures by producing and retaining heat (Heinrich, 1993). These adaptations, however, make them more susceptible to the effects of increased temperature, since they can easily overheat (Williams & Osborne, 2009).

To move through the world and locate floral resources, bumblebees rely on flight, visual and olfactory cues, and cognitive abilities (Gérard et al., 2023). Bumblebees are central place foragers, meaning they depart from their nests in search of nectar and pollen and return

with the rewards (Heinrich, 1976a). On average, foraging trips last 2 hours and they can typically cover large distances and visit many flower patches (Osborne et al., 1999). During these foraging bouts, bumblebees are exposed to variable environmental conditions and understanding how these will affect their behavior and physiology is critical for predicting their future responses to climate change.

Bumblebees provide an excellent model for understanding pollination dynamics and ecology. Studying their thermoregulatory capacities, behavior, foraging patterns, interactions with plants, as well as how they respond to environmental stressors can enhance our understanding of the relationship between pollinators and their floral resources and how it will be affected by climate change stressors.

### *Commercial bumblebees*

Bumblebees have been bred and used in controlled environments for crop pollination since the mid 1980's. It is currently estimated that ~ 2 – 4 million of these commercial bumblebee colonies are used for crop pollination each year (Velthuis & Van Doorn, 2006). The use and trade of commercial bumblebees has been controversial, since there is concern that they threaten wild bumblebee populations by spreading pathogens (Colla et al., 2006), mating with wild conspecifics (Bartomeus et al., 2020), or competing for floral resources (Ishii et al., 2008). However, other studies have also shown that parasite-infected commercial bumblebee do not affect adjacent wild populations (Trillo et al., 2021) and that there is limited introgression and low impact of commercial bumblebee colonies on the genetic integrity of local bumblebee populations (Franchini et al., 2023).

Commercial bumblebees have also become increasingly popular in scientific research over the last decades (Owen, 2016). These bumblebee colonies of different species serve as excellent model systems for multiple reasons. Their ecological importance as pollinators, coupled with the controlled environments in which they are used, offer researchers a level of experimental control that is often challenging to achieve in the wild. In greenhouses or controlled laboratory settings, variables such as temperature, humidity, and floral resources can be manipulated, allowing scientists to design and conduct experiments with precision. Performing experiments in controlled environments is especially advantageous when

investigating specific aspects of bumblebee biology, such as their response to environmental stressors. By studying commercial bumblebees, researchers can gain insights into pollination dynamics, insect behavior, genetic factors, and the impacts of environmental stressors. Ultimately, the knowledge derived from studying these insects contributes not only to the understanding of bumblebee biology but also to the development of strategies for their conservation and sustainable use in agriculture.

Koppert Biological Systems (the Netherlands) and Biobest (Belgium) are the two dominant suppliers of commercial bumblebee colonies in Europe and have played a central role in shaping the pollination services industry since the early 1990s (Velthuis & Van Doorn, 2006). Both companies were among the first to successfully rear *Bombus terrestris* at scale, enabling the widespread adoption of managed bumblebee pollination in greenhouse and polytunnel cultivation systems. Their colonies are now used extensively across the continent to support the production of crops such as tomatoes, peppers, strawberries, and blueberries, particularly under conditions where natural pollinators are scarce or inactive (Nayak et al., 2020). The success of these companies lies not only in their ability to maintain reliable supply chains across diverse agricultural markets, but also in their continued investment in technological innovation to optimize pollination efficiency under artificial and variable environmental conditions. As key actors in the commercial pollination sector, Koppert and Biobest have become integral to the functioning of intensive horticultural production systems throughout Europe. Given their widespread deployment in controlled and semi-controlled environments, it is crucial to understand how environmental variables, such as temperature, affect the behavior and performance of these commercially bred bumblebees.

To better understand how commercial colony foraging dynamics are shaped by temperature, in **Chapter I** we investigated the foraging behavior of commercial bumblebee colonies from the two leading European breeders, Biobest and Koppert. By deploying colonies from both companies at the same outdoor location in Greece, we were able to quantify foraging behavior under identical environmental conditions. Using video observations, RFID tracking, thermal imaging, and temperature loggers, we measured metrics such as departure frequency, foraging duration, pollen collection probability, colony temperature, and worker body temperature upon departure and arrival. Our results showed that Biobest workers

began foraging at cooler temperatures and increased both their foraging duration and pollen collection as environmental temperature rose. In contrast, Koppert colonies displayed relatively stable foraging behavior regardless of temperature, with shorter trips and less temperature-dependent pollen collection (Fig. 1).

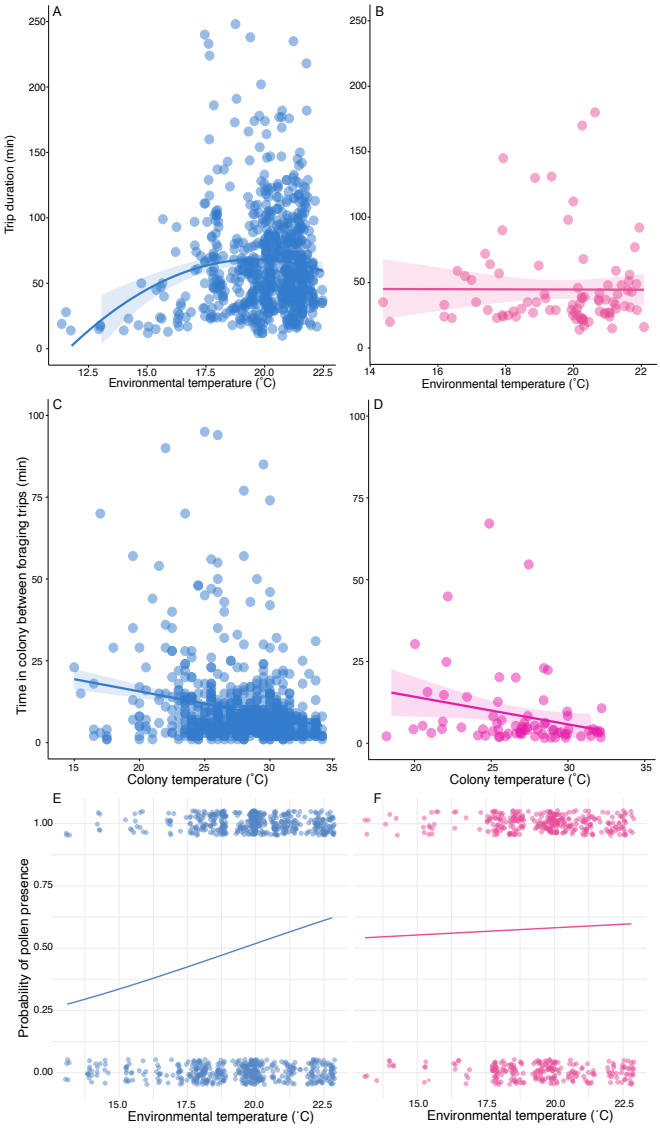


*Figure 1. Environmental temperature and trip duration (A, B), time inside the colony in between foraging trips (C, D), and probability of pollen presence (E, F) for Biobest (blue) and Koppert (pink) bumblebees.*

We also examined internal colony temperature, worker body size, and body temperature to explore potential causes of these behavioral differences. While both Biobest and Koppert colonies showed similar thermoregulatory patterns, Biobest workers were significantly larger and exhibited more variation in size than Koppert workers. We found that the body temperature of departing workers differed between breeders, independent of colony temperature, suggesting physiological or behavioral differences. Our findings highlight that commercial colonies from different breeders can vary in their environmental responses, likely due to differences in rearing practices, colony development stage, or genetic stock. These results underscore the importance of considering breeder-specific traits when selecting colonies for agricultural pollination under varying climatic conditions and the need to further investigate potential physiological, behavioral, morphological, or genetic differences between the two breeders.

## *Physiology and thermoregulation*

### *Colony-level thermoregulation*

Bumblebees (*Bombus* spp.) are known for their remarkable ability to regulate the internal temperature of their nests, a critical factor for colony survival, brood development, and overall productivity (Gradišek et al., 2023). Thermoregulation within the hive is a finely tuned process achieved through both behavioral and physiological mechanisms, allowing colonies to maintain optimal temperatures despite external environmental fluctuations (up to a certain point) (Bretzlaff et al., 2024). Bumblebee colonies must balance the temperature needs of developing brood, the energy demands of adult workers, and the environmental constraints imposed by their surroundings.

One of the primary methods bumblebees use to regulate hive temperature is through metabolic heat production. Worker bumblebees are capable of generating heat by vibrating their thoracic flight muscles in a process called shivering thermogenesis (Heinrich, 1993). This behavior is particularly important during cooler conditions or when the colony requires rapid temperature elevation for brood incubation. Worker bees often cluster around the brood cells and shiver their thoracic muscles to raise the surrounding temperature, ensuring optimal conditions for larval and pupal development. The brood nest typically requires temperatures between 28°C and 32°C for proper growth, and deviations from this range can result in developmental delays or mortality (Vogt, 1986; Weidenmüller et al., 2002; Weidenmüller, 2004).

Conversely, in situations where temperatures exceed optimal ranges, bumblebees employ cooling mechanisms to prevent overheating. Workers can fan their wings at the entrance of the nest, creating airflow that helps dissipate excess heat (Westhus et al., 2013). Additionally, bumblebees may collect water and distribute it throughout the nest to facilitate evaporative cooling, a strategy that is particularly effective under high ambient temperatures (Ferry & Corbet, 1996). These cooling behaviors are essential in maintaining the structural integrity of the wax brood cells and ensuring the health and viability of the developing brood.

Hive architecture also plays a significant role in thermoregulation. Bumblebee nests are typically built in insulated cavities, such as abandoned rodent burrows, which provide a stable microclimate (Liczner & Colla, 2019). The wax canopy constructed by bumblebees over the brood cells acts as an additional insulating layer, helping to buffer against sudden temperature fluctuations. This canopy minimizes heat loss during colder periods and reduces heat gain during warmer conditions, providing a stable environment for brood development (Jones & Oldroyd, 2006).

Colony size and worker density further influence thermoregulation efficiency. Larger colonies with a higher number of workers generally have better thermal stability due to the collective heat produced by the bees' metabolic activity. Smaller colonies, on the other hand, may struggle to maintain optimal temperatures, especially in colder or highly variable climates (Weidenmüller et al., 2022). Worker distribution within the nest is also dynamic, with individuals repositioning themselves to optimize heat transfer to the brood or to participate in cooling activities (Bretzlaff et al., 2023).

Environmental factors, such as ambient temperature, humidity, and nest site selection, directly impact the success of thermoregulation efforts (Bretzlaff et al., 2024). For example, nests located in shaded or underground sites are naturally more insulated from temperature extremes compared to those in exposed areas (Antoine & Forrest, 2021). Similarly, high humidity levels can aid in evaporative cooling, while excessively dry conditions may impede this process (Constable, 2019). Climate change poses a significant threat to hive thermoregulation, as increasing temperature extremes and unpredictable weather patterns may push colonies beyond their physiological limits (Maebe et al., 2021; Bretzlaff et al., 2024; Ostwald et al., 2024).

Thermoregulation is not only vital for brood development but also for colony productivity and survival. When colonies are unable to maintain stable internal temperatures, workers may divert time and energy from foraging to thermoregulatory tasks (Wynants et al., 2021; Bretzlaff et al., 2024). This trade-off can reduce overall colony efficiency, limit resource acquisition, and ultimately impact reproductive success. Furthermore, prolonged exposure to suboptimal temperatures can increase colony stress, weaken immune responses, and make

colonies more susceptible to pathogens and parasites (Palmer-Young et al., 2019; White & Dillon, 2023; Tobin et al., 2024).

In commercial pollination scenarios, thermoregulation becomes even more critical, as colonies are often deployed in artificial environments such as greenhouses, where temperature and humidity levels may differ significantly from natural conditions (Dag, 2008; Rowe et al., 2023). Understanding the thermoregulatory mechanisms of bumblebee colonies can help improve hive design, optimize deployment strategies, and ensure colony resilience under variable conditions. For instance, providing adequate ventilation, shading, or water resources in greenhouse settings can support natural thermoregulatory behaviors and enhance colony performance (Wang et al., 2024).

In conclusion, bumblebee hive thermoregulation is a complex and dynamic process involving behavioral, physiological, and architectural strategies. It is essential for maintaining brood development, colony productivity, and overall resilience under changing environmental conditions. As climate change continues to alter temperature and humidity patterns, understanding and supporting bumblebee thermoregulation will be critical for both wild and commercial colonies. Further research into species-specific thermoregulatory capacities, along with practical applications in agricultural systems, will play a key role in ensuring sustainable pollination services and bumblebee conservation in the future.

### *Bee-level thermoregulation*

Despite sometimes being referred to as “ectotherms,” bumblebees are considered “endo-heterothermic” organisms, capable of thermoregulation (Heinrich, 1972a; Heinrich, 1993; Heinrich, 2009; Woodard, 2017). They can achieve high internal temperatures by buzzing (shivering) and through the excess heat produced by thoracic muscles before or during flight (Heinrich, 1972a; Heinrich, 2009). This capability enables some species to forage in conditions as low as 0 ˚C (Heinrich, 1993; Heinrich & Vogt, 1993; Hines, 2008). In addition to internal heat generation, bumblebees possess external adaptations that aid in cold tolerance; they are covered in a dense coat of long, branched hairs that insulate their bodies and trap warm air close to them. In fact, bees with longer hair have been found to enter chill coma at lower

temperatures than bees of the same size with shorter hair (Church, 1960; Heinrich & Esch, 1994; Peters et al., 2016).

Unlike most other bees, bumblebees have a unique circulatory system that enables them to use a "counter-current heat exchanger" found in the petiole – the region connecting the thorax and the abdomen – for thermoregulation (Heinrich, 1976b; Heinrich & Esch, 1994). Anatomical studies have shown that bumblebees have an aorta that goes from the abdomen and loops around the thorax creating a heat exchanger powered by diaphragm muscles (Heinrich, 1976b; Fig. 2).

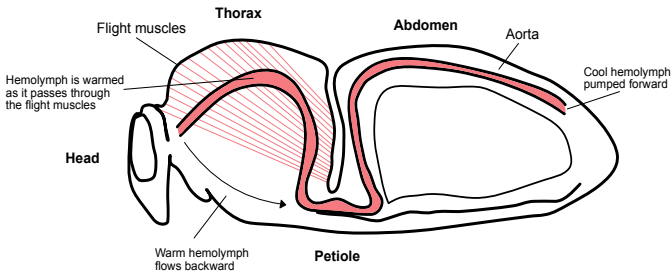


*Figure 2. Bumblebee thermoregulation mechanism, adapted from Heinrich, 1976b.*

In cold conditions, bumblebees can use this counter-current heat exchanger to conserve and recirculate heat generated during flight and, in turn, prevent heat loss, enabling them to operate at temperatures in which other insects would enter a chill coma (Heinrich, 1993). Most research on bumblebee thermoregulation has focused either on colony-level heat regulation or on how individual bees warm up under cold conditions to enable flight (Vogt, 1986; Wynants et al., 2021). It has been hypothesized that, conversely, in warm conditions—such as those during heatwaves or projected future climates—bumblebees may reverse their heat-exchange mechanism, shunting heat from the thorax to the abdomen and/or head (Heinrich, 1972a), where it can be dissipated more effectively. The abdomen, which serves a brood-incubation role, is adapted to dissipate heat at roughly twice the rate of the thorax (Heinrich, 1972b). To date, little work has focused on the effects of increasing environmental temperatures on bumblebee thermoregulation and it remains unclear whether bumblebees are able to use their counter current heat exchanger when overheating as a means of cooling down (Heinrich, 1973).

Heinrich (1974) found that bumblebees of the species *Bombus vosnesenskii* use the counter-current heat exchanger to transfer heat from the thorax to the abdomen. These experiments were conducted on immobile bumblebees by heating up the thorax while measuring abdomen temperature, activity of the heart and the ventral diaphragm, and abdominal pumping (or ventilatory behavior) (Heinrich, 1974). However, experiments conducted on *B. vagans* (Heinrich, 1972a) and *B. terricola* (Heinrich, 1972c) foraging in the field at ambient temperatures, showed that the temperature of the abdomen was independent of thorax temperature and therefore provided no evidence of a counter-current heat exchanger being used to cool down. Later, Baird (1986), proposed a model to estimate whether active heat transfer occurred between the thorax and the abdomen and/or head (which had not been considered in earlier work) based on the following equation:

$$R_{segment} = \frac{(T_{segment} - T_{env})}{(T_{thorax} - T_{env})}$$

where $R_{segment}$ is the excess temperature ratio, $T_{segment}$ is the temperature of the body segment (either the abdomen or head), $T_{thorax}$ is the thorax temperature, and $T_{env}$ is the environmental temperature. If no active heat transfer occurs between the thorax and the abdomen or head, $R_{segment}$ would remain constant across a range of temperatures and indicate only passive heat transfer between body segments. However, if $R_{segment}$ increases as a function of increasing $T_{env}$, it is an indication that active heat transfer is occurring between the thorax and either body segment (Fig. 3).

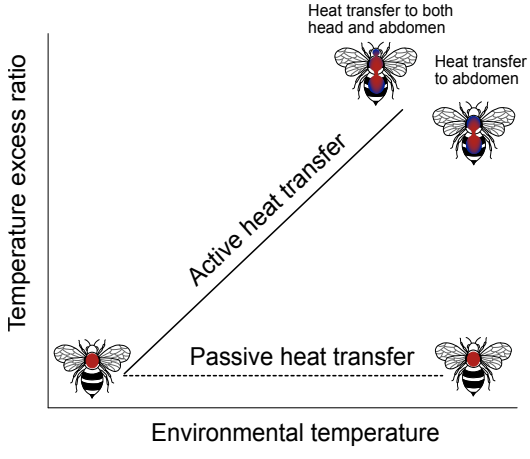


*Figure 3. Temperature excess ratio and environmental temperature.*

This equation does not take into account evaporative heat loss but can be used to provide an indication on whether the abdomen and the head can be used as variable radiators (Baird, 1986). Moreover, studies on bumblebee thermoregulation have not taken into account how this relationship between body temperature and environmental temperature may be affected by behavioral context (i.e., whether the bees are resting, preparing to fly, flying, or post-flight), which could affect whether bumblebees use the head and abdomen for active heat transfer or not.

To address this knowledge gap, in **Chapter II**, we investigated how commercial buff-tailed bumblebees (*Bombus terrestris*) from Koppert (Berkel en Rodenrijs, the Netherlands) regulate body temperature under increasing environmental temperatures and across different behavioral states—resting, pre-flight, and post-flight. Our aim was to identify whether bumblebees actively modulate temperatures in different body parts (head, thorax, and abdomen) as a function of ambient temperature and behavioral activity. To do this, we exposed bumblebee workers to five ecologically relevant temperatures (24 °C to 32 °C) and measured their body temperatures in each state. We predicted that resting bees would conform to ambient temperatures, while pre-flight and post-flight individuals would show evidence of thermoregulation. Additionally, we measured flight speed and foraging activity to explore whether behavioral responses compensate for potential thermal stress.

Our results showed that resting bumblebees closely tracked environmental temperatures across all body parts, suggesting that inactive bees have limited thermoregulatory activity. In contrast, pre-flight and post-flight bumblebees maintained thoracic temperatures significantly above ambient levels, indicating active thermogenesis, which is likely used to prepare for and sustain flight. Notably, post-flight bees also exhibited elevated head and abdominal temperatures, consistent with heat transfer mechanisms that may facilitate cooling (Fig. 4). The excess temperature ratio analysis suggested that active heat shunting from the thorax to other body parts does occur in *B. terrestris*, especially at higher temperatures. We also observed a decline in foraging activity and an increase in flight speed at higher temperatures, suggesting that elevated heat also affects behavior. Together, our findings highlight the nuanced thermoregulatory strategies bumblebees use in response

to warming and suggest potential limits to their performance and survival under future climate scenarios.

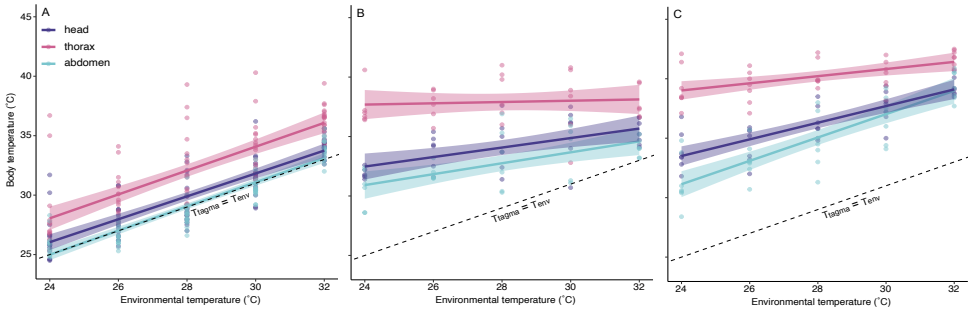


*Figure 4. Body temperature of B. terrestris workers in different behavioral states versus environmental temperature. (A) Resting. (B) Pre-flight. (C) Post-flight. Dashed lines indicate the isometric (same rate) line between body and environmental temperature.*

## *Flight and temperature*

Flight is one of the most energetically demanding and ecologically important behaviors an insect can perform (Reinhold, 1999; Harrison & Roberts; 2000). Understanding the impact of environmental conditions on flight performance is critical not only for understanding the limitations of insect flight under climate change pressures, but also for predicting how environmental services might be affected. In elevated ambient temperatures bumblebees risk overheating due to the excess heat produced by their thorax muscles in flight (Heinrich, 1981). Although understanding the relationship between ambient temperature and flight performance is important for predicting how bumblebee activities will be affected by climate change, few studies to date have focused on this.

Bumblebee foragers must perform careful and precise movements to locate and collect resources from flowers and to return to the hive (Detrain et al., 1999). Insect flight originates from the activity patterns produced by self-organizing neural circuits situated in the thoracic ganglion, known as central pattern generators (CPGs) (Decolmyn, 1980; Eisenhart et al., 2000; MacKay-Lyons, 2002; Bidaye et al., 2018). CPGs are known to be thermosensitive and this sensitivity allows insects to adapt their motor patterns and behaviors in response to variations in temperature (Janssen, 1992; Robertson, 2004; Hückesfeld et al., 2011). Higher temperatures can lead to faster nerve impulses, which may influence the firing rates and coordination of neurons within the CPGs. In turn, this could impact flight control and performance if neural activity is not carefully regulated. To date, few studies have investigated the effects of temperature on insect flight performance and, of these, none have been performed using free-flying insects. The two studies that have investigated temperature and flight performance used insects tethered to flight mills (Spiewok & Schmolz, 2006; Kenna et al., 2021). However, research suggests that tethered flight does not represent the complexities of free-flight, since tethered insects are constrained in their movement, lack realistic environmental feedback, can experience stress, and, in some cases, the flight mill provides support for the insect's weight (Riley et al., 1997; Taylor et al., 2010; Ribak et al., 2017). While Kenna et al. (2021) highlighted the importance of understanding how temperature affects flight in bumblebees, by showing that the optimal temperature for flight performance in *B. terrestris* was ~24 ˚C, the results must be interpreted with caution because

tethered bumblebees may not use their array of thermoregulatory behaviors and mechanisms under such constrained and unnatural conditions.

When a flying insect encounters elevated temperatures beyond their flight performance optima, they could employ different strategies to prevent overheating. To decrease endogenous heat production, they could lower the flight metabolic rate by reducing wing stroke amplitude and wing beat frequency, which would lead to a reduction in flight speed (Glass & Harrison, 2022; Roberts & Harrison, 1999; Roberts et al., 1998). Alternatively, insects could increase their flight speed (as observed in **Chapter II**) to potentially take advantage of the increased convective heat loss that occurs as the thickness of the boundary layer between themselves and the air decreases (Heinrich, 1976; Nicolson & Louw, 1982; Roberts & Harrison, 1998). At present, there is no clear and conclusive evidence that bumblebees employ either of these mechanisms. For example, *B. pascuorum* and *B. pratorum* individuals decreased their wing beat frequency as temperatures increased from 14 ˚C to 21.5 ˚C and from 14 ˚C to 24.5 ˚C, respectively (Unwin & Corbet, 1984). But in *B. vosnesenskii,* flight metabolic rate did not change with air temperature between 10 ˚C and 30 ˚C, suggesting that other mechanisms (such as shunting excess heat to the abdomen or head) may be employed at higher environmental temperatures (Heinrich, 1976) or that different bumblebee species have different strategies for regulating their body temperature.

Overall, there is a need to further investigate the extent to which environmental temperature affects bumblebee flight, and in turn, the pollination services they provide. It is also necessary to better understand the thermoregulatory mechanisms that these insects will use when exposed to unfavorable conditions.

## *Vision and temperature*

Like other neural processes, visual processing is temperature dependent. Previous studies in flies and bumblebees have shown that temperature increases the speed of photoreceptor responses and reduces motion blur (Tatler et al., 2000, Rother et al., 2023). For example, the heat generated by the thorax in walking in bumblebees is sufficient to warm the eyes and increase the photoreceptor temporal resolution (Rother et al., 2023). Up to a certain point, this increase in temperature is beneficial for visual systems, until a limit is reached and the

visual processing deteriorates. When bumblebees fly at high environmental temperatures and shunt excess endogenous heat to the head and abdomen, head temperature may exceed the beneficial temperature to enhance photoreceptor activity and may instead impair vision. Therefore, understanding the thermal limits of neural processes, such as vision, is important to predict how climate change pressures will affect foraging behavior.

Bumblebees experiencing overheating during flight – when average environmental temperature increases or during heatwaves – may be pushed to start foraging earlier in the day when temperatures haven't reached their maximum (Hall et al., 2021). However, flying in these conditions may also prove challenging and the risk of collision might increase due to poor vision (Kelber et al., 2006). Compared to other diurnal insects, bumblebees are relatively good at seeing in dim light because their photoreceptor integration time increases as light intensity decreases, which improves visual sensitivity (Reber et al., 2015). But what happens when bumblebees are pushed to forage when light levels are low but the temperature is high? To date, the synergistic effects of temperature and light availability on visual performance and flight control have not been explored, but understanding the foraging capabilities of bumblebees under these conditions is important to predict their dynamics in future climate systems.

In **Chapter III**, we investigated how rising temperatures and low light levels—two increasingly common environmental conditions under climate change—interact to affect visual processing and flight control in *Bombus terrestris*. Using electroretinography, we found that photoreceptor signal-to-noise ratio (SNR) peaked at intermediate temperatures and declined at both lower and higher temperatures. However, this thermal sensitivity diminished under dim light, where visual reliability was already compromised due to photon limitation. These results suggest, that although higher temperatures can accelerate visual processing in bright conditions, they offer little to no benefit in dim light, where increased neural noise may overwhelm any gains in speed.

Building on these physiological findings, we examined the flight behavior of bumblebees in a tunnel under combinations of bright/dim light and moderate/high temperature. Flight trajectories revealed that bees flew closer to the midline and faster in

bright light as their head temperature increased, consistent with improved visual processing. In contrast, under dim light, neither flight speed nor centering behavior improved with increasing temperature, indicating a plateau in visual performance (Fig. 5). Together, our results demonstrate a non-linear interaction between temperature and light on bumblebee vision and flight, suggesting that future heatwaves occurring during dawn or dusk may degrade foraging efficiency by pushing bees beyond their visual performance limits.

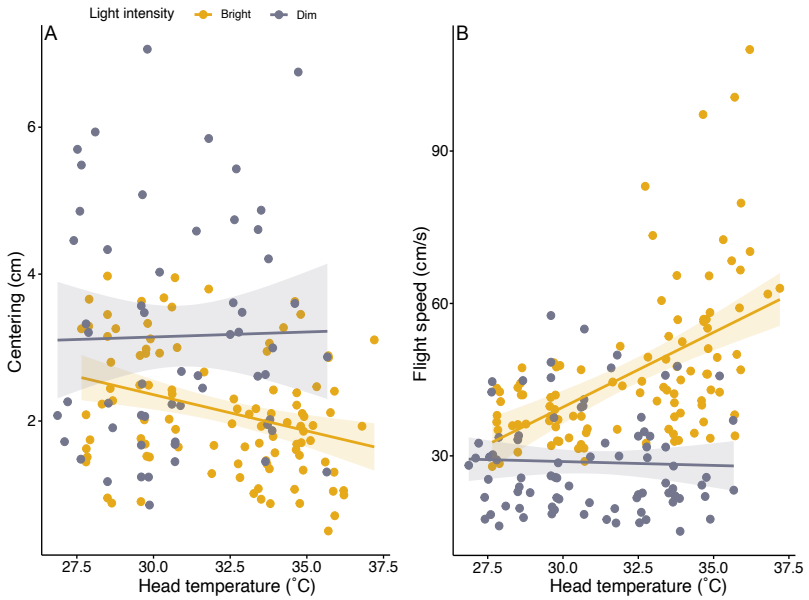


*Figure 5. Flight control components and head temperature. A. Centering (average distance from the midline, cm) and B. Flight speed (cm/s). Bright light (600 lx) is shown in yellow and dim light (4 lx) is shown in gray.*

## *Pollination and temperature*

Pollination is a critical ecological process that ensures the reproduction of many plant species, including those vital for food production (Peixoto et al., 2022). Insect pollinators, such as bees, butterflies, and flies, facilitate the transfer of pollen between flowers, enabling fertilization and seed production (Linhart, 2014). However, climate change—characterized by rising global temperatures, increased frequency of heatwaves, and altered weather patterns—is significantly impacting pollination processes (Reddy et al., 2012; Settele et al., 2016). These temperature-related changes can disrupt insect behavior (Sharma & Singla, 2021), plant-pollinator interactions (Hegland et al., 2009), and overall plant reproductive success (Eckert et al., 2010; Fernández-Pascual et al., 2019), with potential consequences for biodiversity and agriculture.

### *Buzz pollination*

Buzz pollination, or sonication, is a specialized pollination mechanism in which bees use rapid vibrations to extract pollen from flowers with poricidal anthers, structures that release pollen only through small pores or slits (Vallejo-Marín, 2019). Unlike passive pollen release mechanisms, these anthers require a specific vibratory stimulus to dislodge pollen grains (Vallejo-Marín & Russell, 2024). This unique interaction has evolved in thousands of plant species across diverse families, including economically important plants like Solanaceae (e.g., tomatoes, potatoes) and Ericaceae (e.g., blueberries) (De Luca & Vallejo-Marín, 2013). Bumblebees (*Bombus* spp.) are among the most efficient buzz pollinators, generating high-frequency thoracic vibrations to release pollen that would otherwise remain inaccessible to most other pollinators (Vallejo-Marín, 2022). Their ability to produce controlled vibrations and modulate their buzzing behavior makes them particularly effective in pollinating these structurally complex flowers.

The biomechanics of buzz pollination in bumblebees are driven by their indirect flight muscles, which can be decoupled from the wings to generate powerful, non-flight vibrations (Brito et al., 2020; Vallejo-Marín et al., 2024). These vibrations are transmitted through the bee's body to the anthers, causing pollen grains to be ejected in a process often compared to shaking salt from a container. Recent studies have shown that bumblebees can fine-tune their

buzzing frequency and amplitude based on floral traits, optimizing pollen release while minimizing energy expenditure (Pereira Nunes & Vallejo-Marín, 2022). This level of control suggests a high degree of sensory-motor integration in buzz pollination, allowing bumblebees to adjust their behavior in response to environmental conditions such as temperature and humidity, which can influence pollen availability and viscosity.

Temperature plays a crucial role in shaping the efficiency of buzz pollination, as it affects both the biomechanics of bumblebee vibrations and the physical properties of pollen. At lower temperatures, muscle contraction efficiency declines, potentially reducing the amplitude and frequency of buzzing vibrations. Conversely, at elevated temperatures, flight muscles may overheat, potentially affecting coordination and limiting the duration of effective sonication. In the context of climate change, increasing temperatures and unpredictable weather patterns may disrupt the delicate balance between pollinators and their floral resources. If rising temperatures alter the buzzing efficiency of bumblebees, this could have cascading effects on plant reproductive success, especially for crops and wild plants that rely exclusively on buzz pollination.

Beyond its ecological importance, buzz pollination has significant agricultural implications, particularly in controlled environments such as greenhouses (Cooley & Vallejo-Marín, 2021). While honeybees (*Apis mellifera*) are widely used for commercial pollination, they are largely ineffective at buzz pollination due to their inability to generate the necessary vibrations (Vallejo-Marín, 2019). As a result, bumblebees have become the primary managed pollinators for many solanaceous crops, enhancing fruit yield and quality (Nayak et al., 2020; Abrol et al., 2021). Understanding how environmental factors, including temperature fluctuations, affect buzz pollination dynamics is critical for ensuring the stability of both natural and agricultural ecosystems. As climate change continues to alter environmental conditions, further research into the resilience and adaptability of bumblebees in the context of buzz pollination will be essential for predicting and mitigating potential disruptions to pollination services.

In **Chapter IV**, we investigated how heatwaves impact the pollination behavior of bumblebees and the consequences for plant reproductive success. We focused on *Bombus terrestris* from Koppert Biological Systems, and *Solanum rostratum*, a buzz-pollinated plant.

By simulating heatwave conditions in a controlled foraging arena, we measured changes in bumblebee foraging behavior, including visitation rate, duration and number of foragers, and assessed their effect on fruit and seed set. We found that high temperatures reduced foraging activity, leading to fewer visits and shorter visitation times. This behavioral shift significantly lowered fruit and seed production in *S. rostratum*, suggesting that even short-term exposure to heatwave conditions can compromise pollination success and reproductive output in buzz-pollinated plants (Fig. 6).

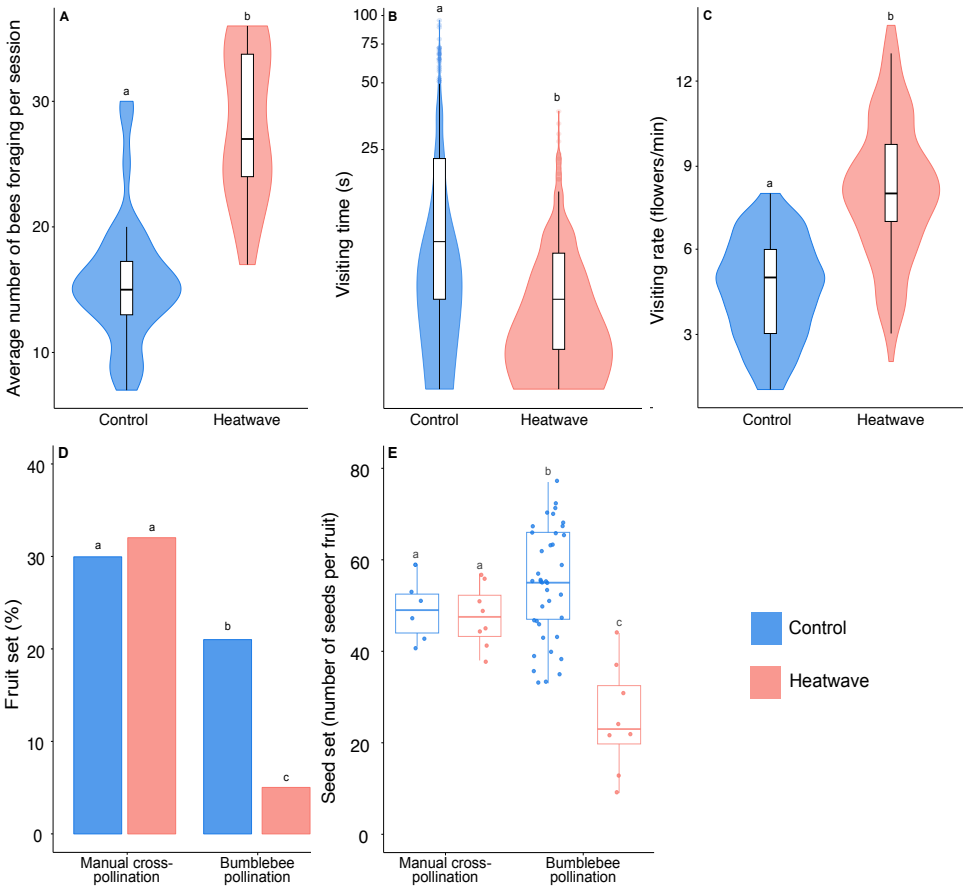


*Figure 6. The impact of simulated heatwaves on A) the average number of bees foraging per day, B) visiting time (s) (n = 994), C) visiting rate (number of flowers visited/min) (n = 370), D) fruit set: the percentage of fruit developed (n = 565) and E) seed set: number of seeds per fruit (n = 62) in manual cross-pollinated and bumblebee-pollinated plants under control (blue - 26 ˚C:20 ˚C, day:night) and heatwave (red - 32 ˚C:26 ˚C, day:night) periods. Different letters indicate statistically significant difference under control (blue - 26 ˚C:20 ˚C, day:night) and heatwave (red - 32 ˚C:26 ˚C, day:night) temperatures. Different letters indicate statistically significant difference of $p < 0.05$.*

To understand the underlying mechanism, we tested how temperature affects the biomechanics of buzz pollination. Using high-resolution accelerometers and thermal imaging, we quantified the vibrations produced by bumblebees during floral buzzing across a temperature gradient. We found that higher temperatures reduced the amplitude, frequency, and duration of floral vibrations, which in turn led to a significant decrease in pollen release (Fig. 7). These results suggest that thermal stress impairs the muscular performance needed for effective buzz pollination. Our findings reveal that rising temperatures, particularly in the form of heatwaves, can disrupt both behavioral and mechanical aspects of pollination, reducing pollen transfer and reproductive success. This highlights a key vulnerability in plant-pollinator systems and raises concerns about the resilience of biodiversity and crop productivity under climate change.

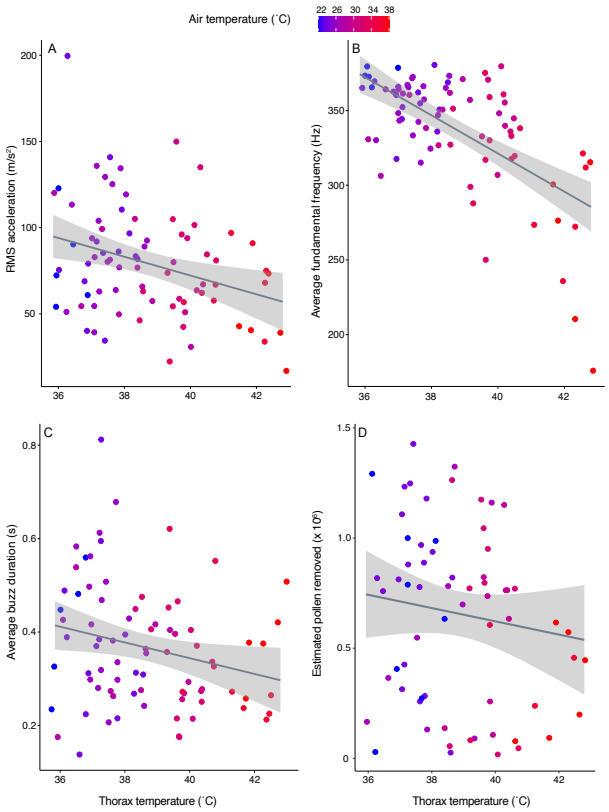


*Figure 7. The effect of temperature on the properties of bumblebee buzz pollination. A) Root mean square amplitude (m/s2), B) fundamental frequency (Hz), C) buzz duration (s) and D) estimated number of pollen grains removed. Colors correspond to the different air temperature treatments.*

# Concluding remarks and future directions

Overall, this thesis has investigated how environmental temperature influences bumblebee behavior, physiology, and pollination performance, with a focus on commercial colonies of *Bombus terrestris*. Across four chapters, we examined how temperature shapes foraging dynamics, thermoregulation, sensory processing, flight control, and pollination effectiveness. Together, these studies provide a multi-level perspective on the thermal sensitivity of bumblebees and reveal potential vulnerabilities in pollination systems under future climate change scenarios.

Our findings demonstrate that commercial bumblebee colonies from different breeders exhibit markedly different foraging responses to temperature. These differences are likely rooted in variation in body size, physiology, or genetic background, and emphasize the need to account for breeder-specific traits when deploying colonies for agricultural pollination. Beyond colony-level variation, we showed that bumblebee workers actively regulate body temperature during foraging, particularly in the thorax, but may also shunt heat to the head and abdomen as ambient temperatures rise, highlighting a potentially important but understudied thermoregulatory strategy in high-temperature environments.

In addition to behavioral and physiological responses, we found that high temperatures do not uniformly enhance visual processing; rather, their effects depend on ambient light. Under dim conditions, such as those during early morning or late evening foraging, elevated temperatures failed to improve flight performance, likely due to compounded sensory noise. This indicates a non-linear interaction between temperature and light that may limit bumblebee effectiveness during critical foraging windows in future climates.

Finally, we showed that heatwaves impair not only foraging behavior but also the mechanical production of floral vibrations required for buzz pollination. The resulting decline in pollen release and fruit and seed set underscores the potential for acute thermal events to disrupt key ecosystem services and agricultural productivity. These findings suggest that pollination systems relying on buzz-pollinating bees may be particularly vulnerable to climate extremes.

Future work should aim to further disentangle the physiological, morphological, and genetic factors that underlie variation in thermal sensitivity among commercial colonies. Understanding the heritability and plasticity of these traits could inform breeding programs aimed at developing heat-resilient pollinators. Additionally, more research is needed on the potential for acclimation and adaptation to novel thermal regimes, both at the individual and colony level. Given the increasing frequency of extreme weather events, integrating thermal performance metrics into pollinator risk assessments will be essential for predicting and mitigating climate change impacts on biodiversity and food security.

By highlighting the complex effects of temperature on bee behavior, physiology, and pollination, this thesis contributes to a growing body of evidence that climate change poses multifaceted challenges to insect-mediated ecosystem services. Addressing these challenges will require interdisciplinary approaches that bridge behavioral ecology, thermal biology, agricultural sciences, and conservation policy.

# Populärvetenskaplig sammanfattning

Denna avhandling undersöker hur temperatur påverkar humlors beteende, fysiologi och pollinationsförmåga, med särskilt fokus på kommersiella kolonier av *Bombus terrestris*. Genom fyra kapitel analyseras hur värme (och ljus) samverkar och påverkar humlors förmåga att reglera kroppstemperatur, orientera sig, flyga och effektivt pollinera blommor.

I **kapitel I** jämfördes födosöksbeteendet hos humlekolonier från de två största europeiska producenterna, Biobest och Koppert, under identiska fältförhållanden. Resultaten visade att Biobest-arbetare började flyga vid lägre temperaturer och ökade både sin insamlingsfrekvens och polleninsamling med stigande temperatur. Koppert-kolonier visade däremot ett mer stabilt beteende, med kortare turer och mindre temperaturberoende polleninsamling. Skillnader i kroppsstorlek och kroppstemperatur tyder på fysiologiska eller genetiska variationer mellan kolonierna.

I **kapitel II** undersöktes hur humlor reglerar sin kroppstemperatur vid olika omgivningstemperaturer och aktivitetsnivåer. Resultaten visade att inaktiva humlor anpassade sin kroppstemperatur till omgivningen, medan aktiva humlor upprätthöll en högre temperatur i bröstpartiet (thorax), nödvändig för flygförmåga. Vid höga temperaturer verkade humlor även omfördela överskottsvärme till huvudet och bakkroppen – en möjlig mekanism för undvika överhettning.

**Kapitel III** visade att värme påverkar humlors syn och flygbeteende beroende på ljusförhållanden. Under starkt ljus förbättrades flygprestationen med stigande temperatur, men under svagt ljus uteblev denna effekt – sannolikt på grund av ökad brus i nervsystemet. Detta tyder på att framtida värmeböljor, särskilt i gryning och skymning då ljus är svagare, kan försämra humlors orienteringsförmåga och därmed deras effektivitet som pollinatörer.

I **kapitel IV** undersöktes hur värmeböljor påverkar både humlors beteende och de biomekaniska aspekterna av surrpollinering, där vibrationer frigör pollen från blommor. Höga temperaturer minskade både antalet besök och kvaliteten på surren, vilket ledde till lägre frö- och fruktsättning i *Solanum rostratum*. Detta visar att kortvariga värmeböljor kan få betydande negativa effekter på växtpollinering och reproduktion.

Sammanfattningsvis visar denna avhandling att stigande temperaturer kan påverka humlor på flera nivåer: från fysiologi och sensorik till beteende och pollineringsförmågan. Resultaten understryker behovet av att ta hänsyn till värmetålighet hos olika kommersiella kolonier och att vidare studera anpassningsförmåga och genetisk variation för att säkerställa pollineringstjänster i ett förändrat klimat.

# Literature cited

Note: this thesis, including its introductory text (kappa), builds partly upon Guadalupe Sepulveda's licentiate thesis (defended on January 23rd, 2024). Of the chapters included in this thesis, Chapter II and Chapter III wer part of the licentiate thesis, with contributions as follows:

Chapter II: An earlier version of this chapter was included in the licentiate thesis.

Chapter III: An earlier version of this chapter was included in the licentiate thesis. For the current doctoral thesis, analyses have been rerun and text has been rewritten.

Within the doctoral thesis kappa, much of the text in the section "Introduction" is reused from the licentiate thesis kappa. The text has been edited to include new literature and place it into the context of the larger body of work presented in the doctoral thesis.

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