

**From montane meadows to metropolis:
cavity-nesting bees and wasps in a warming world**

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Abstract

Climate change has been linked to widespread changes in the abundances and distributions of many organisms across large spatial scales, yet in many cases, the local ecological processes driving these patterns are poorly understood. This thesis documents the findings of four field studies that characterize the fitness consequences of local environmental variation for cavity-nesting bees and wasps observed in their natural habitats. In doing so, it identifies potential processes that may underlie large-scale relationships between climate variables and wild bees and wasps. Across chapters, several potential processes emerge, involving both intrinsic (physiological) and extrinsic factors. Chapter 1 suggests that warmer daytime temperatures experienced by individuals initiating nests late in the season reduced longevity, which in turn was linked to decreased lifetime reproductive output. Chapter 2 shows that brood cell production by nesting females decreased significantly in hotter, drier summers, partly due to drought-driven reductions in floral host-plant availability. Chapter 3 suggests that the extent to which cavity-nesting bees and wasps can track their climatic niches via range shifts to higher elevations may be limited by the lack of wood substrates beyond local treelines. Finally, Chapter 4 considers the consequences of elevated nest temperatures for juvenile development in cavity-nesting bees and wasps. The data did not reveal a strong effect of nest temperature on juvenile body mass; however, I highlight the potential importance of local vegetation as a thermal buffer given projections of significantly warmer conditions in the coming years. Studies that directly link fitness parameters to climate drivers in natural populations are rare but may provide valuable information for designing effective conservation strategies and informing predictions regarding the capacity of species to respond adaptively to climate change. My thesis contributes to this body of research and highlights the importance of observational studies grounded in natural history.

Résumé

Le changement climatique a été associé à des modifications généralisées de l'abondance et de la répartition de nombreux organismes à grande échelle spatiale, mais dans de nombreux cas, les processus écologiques locaux à l'origine de ces tendances sont mal compris. Cette thèse présente les résultats de quatre études de terrain qui caractérisent les conséquences des variations environnementales locales sur la condition physique des abeilles et des guêpes nichant dans des cavités, observées dans leur habitat naturel. Ce faisant, j'identifie les processus potentiels qui pourraient sous-tendre les relations à grande échelle entre les variables climatiques et les abeilles et guêpes sauvages. Au fil des chapitres, plusieurs processus potentiels émergent, impliquant à la fois des facteurs intrinsèques (physiologiques) et extrinsèques. Le chapitre 1 suggère que les températures en journée plus chaudes subies par les individus qui commencent à construire leur nid tard dans la saison réduisent leur longévité, ce qui est lié à une diminution de leur production reproductive au cours de leur vie. Le chapitre 2 montre que la production de cellules de couvain par les femelles nicheuses diminue considérablement lors des étés plus chauds et plus secs, en partie à cause de la réduction de la disponibilité des plantes hôtes florales due à la sécheresse. Le chapitre 3 suggère que la capacité des abeilles et des guêpes nichant dans des cavités à suivre leurs niches écologiques en se déplaçant vers des altitudes plus élevées pourrait être limitée par le manque de substrats ligneux au-delà de la limite forestière. Enfin, le chapitre 4 examine les conséquences de l'élévation de la température des nids sur le développement des juvéniles chez les abeilles et les guêpes nichant dans des cavités. Les données n'ont pas révélé d'effet significatif de la température du nid sur la masse corporelle des juvéniles ; cependant, je souligne l'importance potentielle de la végétation locale en tant que tampon thermique, compte tenu des prévisions de conditions nettement plus chaudes dans les années à venir. D'une manière générale, les études qui établissent un lien direct entre les paramètres de condition physique et les facteurs climatiques dans les populations naturelles sont rares, même si ces informations peuvent (en principe) être cruciales pour concevoir des stratégies de conservation efficaces et peuvent aider à éclairer les prévisions concernant la capacité des espèces à persister ou à s'adapter au changement climatique. Ma thèse contribue à cet ensemble de recherches et souligne l'importance des études observationnelles fondées sur l'histoire naturelle.

Merci beaucoup à Dr. Michela Dumas pour son aide dans la traduction de ce résumé.

Resumen

El cambio climático se ha relacionado con cambios generalizados en la abundancia y distribución de muchos organismos a gran escala espacial, pero en muchos casos se desconocen los procesos ecológicos locales que impulsan estos patrones. Esta tesis documenta los resultados de cuatro estudios de campo que caracterizan las consecuencias de la variación ambiental local para las abejas y avispas que anidan en cavidades, observadas en sus hábitats naturales. Al hacerlo, identifica los posibles procesos que pueden subyacer a las relaciones a gran escala entre las variables climáticas y las abejas y avispas silvestres. A lo largo de los capítulos, surgen varios procesos potenciales, que implican factores tanto intrínsecos (fisiológicos) como extrínsecos. El capítulo 1 sugiere que las temperaturas diurnas más cálidas experimentadas por los individuos que inician sus nidos a finales de la temporada redujeron su longevidad, lo que a su vez se relacionó con una disminución de la producción reproductiva a lo largo de su vida. El capítulo 2 muestra que la producción de celdas de cría por parte de las hembras que anidan disminuyó significativamente en los veranos más calurosos y secos, en parte debido a la reducción de la disponibilidad de plantas hospedadoras florales provocada por la sequía. El capítulo 3 sugiere que la capacidad de las abejas y avispas que anidan en cavidades para seguir sus nichos ecológicos mediante desplazamientos a altitudes más elevadas puede verse limitada por la falta de sustratos de madera más allá de la línea de árboles. Por último, el capítulo 4 analiza las consecuencias del aumento de la temperatura de los nidos para el desarrollo de las crías de abejas y avispas que anidan en cavidades. Los datos no revelaron un efecto significativo de la temperatura del nido en la masa corporal de las crías; sin embargo, destaco la importancia potencial de la vegetación local como amortiguador térmico, dadas las previsiones de un calentamiento significativo en los próximos años. En términos generales, los estudios que relacionan directamente los parámetros de aptitud física con los factores climáticos en las poblaciones naturales son poco frecuentes, a pesar de que esta información puede ser crucial para diseñar estrategias de conservación eficaces y puede ayudar a fundamentar las predicciones sobre la capacidad de las especies para persistir o responder de forma adaptativa al cambio climático. Mi tesis contribuye a este conjunto de investigaciones y destaca la importancia de los estudios observacionales basados en la historia natural.

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Land Acknowledgement

The sites described in Chapters 1–3 are situated on the traditional territories of the Tabeguache Ute band (Núu-agma-tuvu-pu). Over the course of the 19th century, Ute territories were invaded by white settlers and mining prospectors backed by the U.S. government. Treaty agreements were violated, and the Utes were murdered or forcibly removed from their territories. The Rocky Mountain Biological Laboratory (Gothic, Colorado) was a mining town until the late 1800s. Much of the mining town infrastructure was retained and converted into research station infrastructure such as housing for researchers, laboratories and administration spaces.

The sites described in Chapter 4 are in Tkaronto (Toronto) and Odawa (Ottawa). Tkaronto is the traditional territory of the Mississaugas of the Credit, the Anishnabeg, the Chippewa, the Haudenosaunee, and Wendat peoples. It is now home to many diverse First Nations, Inuit, and Métis peoples. Currently, Tkaronto is thought to be covered by Toronto Purchase, 1805 (Treaty 13) with the Mississaugas of the Credit. Odawa is situated on the unceded, unsundered territory of the Anishinaabe Algonquin Nation, meaning that the land was never legally sold to the crown.

By having conducted research in all of these places, I am a direct beneficiary of colonialism both historical and ongoing. I also acknowledge that the language, scientific approaches and methods of data interpretation I use throughout this thesis reflect a knowledge system founded on the worldviews of those who colonized these lands. I am reflecting on my role in perpetuating colonialism in ecological research, educating myself about the history of the lands I live and work on, finding ways to give light to different ways of seeing the world, and doing my best to come into good relationship with the land following the leadership of her original caretakers.

Acknowledgements

I am very fond of stories. I enjoy reading and listening to them, conjuring them in my mind and writing them (or wishing I had time to write them). Over the past few years, I have been rather occupied with writing the story in this thesis. The story takes place in mountains and cities. The protagonists are bees, wasps, and flowers. The plot revolves around how they might feel about life in a rapidly warming and drying world. This story is a story within another story. The outer story also takes place in mountains and cities. The characters are humans, and the plot revolves around the characters telling the inner story. This outer story hasn't quite concluded yet, and I have not even attempted to begin writing it. This thesis only contains my telling of the inner story, but I would like to include a sketch of the characters in the outer story because their contributions so deeply enriched the writing of the inner story and made it possible for me to tell it.

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but over the past few years, your poetry and music found their way to me and always gave me just enough light to carry on whenever the weight of difficult happenings in the world and in my own life seemed to overwhelm.

To my family—my grandparents, my late Yeh Yeh (爷爷) and Mah Mah (嬷嬷), Gung Gung (公公) and late Poh Poh (婆婆) and my parents Bah-bi and Mama, I would not have had the privilege of coming on this journey had you not made your own journeys to Canada, and once here, worked tirelessly to make life possible, interesting, nurturing, and beautiful for my siblings and me. Bah-bi and Mama, so many of your stories are in here in some way or other—they have made both the inner and outer stories unique and ones that I am proud to tell. To my siblings, Zjae Zjae (姐姐), Justin and Naomi, brother-in-law Justin-Owl, and niece little Juniper, thank you for bringing so much joy and meaning into my life by way of feathered and furry friends, vegetable beds, compost heaps, juggling tricks, frisbee, music, and wooden piggies. I am smiling in thinking of you as I write this.

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To all of you, I have been so honoured and privileged to have been able to add every one of you as characters in this story. You have each brought so much life to this story—both the inner and the outer. I hope there will be many more shared adventures to come.

Dedication

This thesis largely focuses on the lives of female solitary bees and wasps—the matriarchs of bee and wasp world. This thesis is dedicated to four matriarchs in my life:

To Jane, an *Osmia coloradensis* marked blue (2019),
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more, for keeping me company during research presentations, and for
reminding me that an “average” never tells the full story.

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*It is best to look at everything in the world backwards,
upside-down and inside-out before settling too much on an idea.
You may find you never quite settle on anything, and that is rather beautiful.*

~Lee Maracle

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General introduction

Background

The relationships between climate and the abundances and distributions of plants and animals have long been a central theme in ecology. Early written work on this topic dates back to the eighteenth- and nineteenth-century works of botanists and geographers such as Alexander von Humboldt, who was among the first to use instrumentation to quantify abiotic variables (e.g., temperature) and link variation in these factors to species abundances and distributions (von Humboldt and Bonpland 1807, von Humboldt 1849). The role of climate in shaping patterns of biodiversity was further developed over the twentieth century by numerous other individuals. These include Arthur Tansley, who coined the term “ecosystem” to describe the relationships between biotic and abiotic elements as an integrated system (Tansley 1935); Robert Whittaker, who developed “gradient analysis” to quantify relationships between plant community composition and environmental gradients (Whittaker 1967, 1970); and Margaret Davis, whose work with fossil pollen in sediments showed that post-glacial migration patterns of trees reflected species-specific responses to climate (in addition to their dispersal capacities; Davis and Shaw 2001). Other individuals during this time offered more mechanistic frameworks to explain the correlative patterns of species assembly described by their contemporaries; Victor Shelford’s “Law of Tolerance” linked species abundances to their ability to survive, grow, and reproduce over a range of environmental gradients (Shelford 1913), while George E. Hutchinson’s niche concept (Hutchinson 1957) suggested that species persistence in any given location is determined by their specific set of abiotic requirements (i.e., the “fundamental niche”) combined with biotic constraints such as competition (i.e., the “realized niche”).

All of these individuals helped to establish the importance of climate in shaping species abundances and distributions. Notably, implicit in much of their writing was the assumption that the patterns of species distributions they observed reflected the adaptations of organisms to relatively stable local environmental conditions—a premise that may no longer hold given contemporary climate change. Since von Humboldt’s time, global surface temperatures have risen by 1.1 °C due principally to greenhouse gas emissions from human activities over this period (Calvin et al. 2023). The warmest years on record have all occurred within the last decade (NOAA National Centers for Environmental Information 2025), and average temperatures are projected to continue rising at a rate of 0.15–0.25 °C per decade (Calvin et al. 2023). These rising temperatures have been accompanied by significant increases in the frequency and severity of climate and weather extremes such as droughts, heatwaves, floods, and storms (Calvin et al. 2023). This pace of environmental change likely exceeds the rate at which many organisms can adapt or

disperse to track suitable climate conditions. Indeed, the ecological consequences of climate change have already become apparent for many taxa, manifesting in shifts in phenology (e.g., timing of migration, budding and flowering, laying and hatching, emergence), changes in population dynamics (e.g., sex ratios, reproductive success, extinctions), range shifts and range contractions, as well as genetic and physiological responses (Menzel and Fabian 1999, Parmesan and Yohe 2003, Both et al. 2004, Thomas et al. 2004, Parmesan 2006, Hulin et al. 2009, Chen et al. 2011, Bellard et al. 2012, Rodriguez-Dominguez et al. 2019, Horton et al. 2020).

Insects, which constitute an estimated eighty percent of all extant animal species (Wilson, 1992), may be especially sensitive to climate change given that their life-histories (e.g., growth, survival, reproduction) are often strongly influenced by their immediate environmental surroundings (Angilletta 2009, Dillon et al. 2010, Hoffmann et al. 2013). Population- and community-level responses to changes in climate may also manifest more rapidly in insects compared to longer-lived vertebrates due to their short generation times and high reproductive rates (Stange and Ayres 2010, Boggs 2016). Given the significant ecological contributions of insects in many ecosystems as herbivores, decomposers, predators, parasites, seed dispersers, pollinators, and the like (Kim 1993, Losey and Vaughan 2006), the impacts of climate change on insects may have cascading effects on the populations of many other organisms and overall ecosystem functioning.

Wild (undomesticated) bees and wasps play significant ecological roles in many ecosystems. Bees are the primary pollinators of most angiosperms, which make up the majority of vascular plants globally (Buchmann and Nabhan 1996, Kearns and Inouye 1997). Wasps play important regulatory roles as most species are predators or parasites of other arthropods, in addition to contributing to pollination (Brock et al. 2021, Fei et al. 2023, Pereira 2025). Over recent decades, anthropogenic pressures such as habitat loss, pesticide use, invasive species, and pathogens have been linked to significant declines in the populations of many species in both these groups (although there is comparatively little known about wasps; Dejean et al., 2022; Goulson et al., 2015; Potts et al., 2010; Whitehorn et al., 2012). Climate change is a recent addition to this list of threats and its consequences for bee and wasp populations are still unclear, possibly because climate variables may interact and covary with all the aforementioned stressors (Knight et al. 2018). Moreover, the responses of bees and wasps to changes in climate can vary substantially across species and habitats in both direction and magnitude, likely due in part to the immense diversity of morphologies, physiological traits, life-histories, nesting habits, resource specialization, and behavioural adaptations exhibited by these two groups of insects (Kammerer et al. 2021, Pardee et al. 2022, Kazenel et al. 2024).

The impacts of temperature variation on wasps and (especially) bees have been examined in a number of studies that include a mix of laboratory, field, and modelling approaches. Earlier work primarily focused on establishing ideal conditions for the maintenance of domesticated bee populations in agricultural contexts, while the aim of many recent studies has shifted towards elucidating the realized and future impacts of climate change. Lab studies, which generally focus on individual-level physiological responses, have demonstrated strong impacts of temperature on various aspects of bee and wasp life-histories, such as growth, development, body size, timing of emergence, voltinism, survival, and longevity (e.g., Bosch & Kemp, 2003; Li et al., 2021; O'Neill et al., 2023; Radmacher & Strohm, 2010; Schenk, Mitesser, et al., 2018; Stephen, 1965). Field studies, which focus on population- or community-level responses, have offered a broader understanding of the ecological consequences of temperature variation for these insects, with some suggesting that climate conditions can be a predictor of local bee and wasp abundance and diversity (Papanikolaou et al. 2017, Hamblin et al. 2018, Pardee et al. 2022, Casanelles-Abella et al. 2024) and that physiological processes may underlie these patterns (Kazenel et al. 2024). The consequences of local climate variation for other ecological processes such as foraging activity, phenology, nesting preferences, and interactions with competitors and parasites have also been documented (Stone 1994, Forrest and Chisholm 2017, CaraDonna et al. 2018, Wilson et al. 2020, Aung et al. 2022). Species distribution models have further extended population and community-level studies to the geographic distributions of these insects in relation to climate conditions across broader spatial and temporal scales and have suggested that the ranges of a number of species have not shifted in accordance with changes in climate (e.g. Faleiro et al., 2018; Guo et al., 2010; Kerr et al., 2015; Kuhlmann et al., 2012; Soroye et al., 2020; Zhang et al., 2024).

While the findings of all these studies collectively indicate that climate change is having, or will have, significant consequences for wild bees and wasps, the processes underlying the relationships between climate change and the demographic success of these insects remain unclear. The findings of lab studies suggest that physiological mechanisms are likely at play; however, the extent to which these relationships can be extrapolated to natural populations may be limited given the simplified environments of most lab experiments. Variables such as species interactions, resource availability, habitat heterogeneity (e.g., microclimates), and behavioural adaptations may moderate relationships between temperature and the physiological responses of bees and wasps yet are generally challenging or impossible to account for in the lab. Field studies that capture the effects of temperature on variables such as foraging behaviour, phenology, and species interactions offer potential ecological mechanisms to explain climate-driven changes in bee and wasp populations; however, population-level inferences based on these studies are

limited, since the fitness consequences of their relationships with temperature are not captured in most studies (but see Minckley et al. 1994, Farzan and Yang 2018). Finally, field studies and distribution models that characterize relationships between climate variation and bee and wasp communities (often considering many species in aggregate) provide important insight on the cumulative outcome of climate change for the abundances and distributions of these insects at broader spatial scales. Nevertheless, the underlying processes driving the patterns they report may be difficult to decipher given that bees and wasps may respond to environmental variation at much smaller, localized spatial scales relative to what is considered in these studies.

Observational studies that characterize the fitness consequences of climate variation (captured at spatiotemporal scales relevant to the focal taxa) may help to uncover the ecological processes underlying large-scale patterns of abundance and diversity in wild bees and wasps. Such studies can also account for species' physiology, behaviour, life-history, and inter- or intraspecific interactions, thereby connecting findings from the kinds of lab, field, and modelling studies described above. Field observations may also be better able to incorporate nuances of species–temperature relationships such as the indirect effects of climate mediated by other variables (e.g., resource availability) and the consequences of warming for different life-stages, all while considering the unique natural history traits of different species, populations, and habitats. Relatively few field studies have directly quantified the fitness consequences of variation in climate variables for bees, and there is almost no information on wasps—despite the fact that this information may be the most direct indicator of how populations will respond to further warming and could provide practical information for conservation action.

Objectives

This thesis comprises four observational field studies that examine the fitness consequences of variation in local climate variables (primarily temperature) for wild populations of bees and wasps. I focus primarily on female brood production (i.e., reproductive output) as an indicator of fitness; however, I also examine the effects of temperature on other related parameters such as longevity, nest occupancy, developmental success, and juvenile body size. Moreover, although temperature features as a recurring motif throughout this thesis, the impacts of variation in precipitation on bee reproduction—a sometimes-neglected component of our changing climate—are also considered. I also evaluate the roles of other variables that may mediate or moderate the effects of climate, including the constraints of growing-season length, floral resource abundance, the availability of nesting habitat, and local vegetation. Incorporating these environmental variables can allow us to examine the potential indirect effects of climate change. As

much as possible, the environmental predictors in each study are characterized in a way that reflects the natural history traits of the focal taxa; for example, the host-plant specializations of different bee species are reflected in metrics of floral abundance. In essence, the goal of this thesis is to “see the world as they see it”.

I note here that the extent to which climate change is invoked as the main motivation for the four studies varies for the reason that this thesis does not directly quantify the consequences of climate change for bees and wasps *per se*; strictly speaking, “climate” is defined by temperature and precipitation conditions (along with other variables) averaged over broader spatiotemporal extents than what is mostly considered here. Instead, this thesis documents the fitness consequences of natural variation in climate variables observed over smaller, local spatiotemporal scales and uses manipulation of bee and wasp nesting habitat to make inferences about the potential consequences of climate change. Given this approach, in the initial conception of each study, I tried to consider all possible outcomes in the focal taxa’s responses to warmer temperatures, recognizing that climate change could provide short-term fitness benefits depending on the taxon or habitat in question.

Study sites

The first three studies take place in the West Elk mountains of central-western Colorado. In recent years, the state of Colorado, along with much of the Southwest United States have sustained significant changes in climate means and extremes including severe drought events, prolonged heatwaves, and dramatically reduced snowpack and summer rainfall (Rhoades et al., 2018; Zhang et al., 2021). These conditions are projected to intensify in the coming decades (Wahl et al. 2022), but have already resulted in considerable ecological and economic consequences (Bauman et al., 2013; Peltier et al., 2016). Montane ecosystems in this region may be especially vulnerable given that rates of warming may be amplified at high elevations (Trew and Maclean 2021). At the same time, mountains can be practical locales for studying the ecological consequences of climate change because large temperature differences are compressed into short distances along elevation gradients, facilitating studies that employ space-for-time substitution. Data for my thesis were collected in montane meadows in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (2900 m a.s.l.). This region is the traditional territory of the Tabeguache Ute band (Núu-agma-tuvu-pu; see “Land Acknowledgement”) and has experienced relatively little disturbance by way of urbanization and intensive agriculture. I was therefore able to examine the effects of rising temperatures on bee and wasp populations independently of land-use change as well as other potential stressors such as pesticides, pollution, and competition with domesticated honey bees. The

RMBL is also the site of several long-term datasets capturing the abundances and activity periods of various organisms in the area, along with changes in climate. I leverage some of these datasets in my thesis and describe them in greater detail in the chapters themselves.

While the RMBL provides a unique opportunity to examine the ecological consequences of climate variation independently of major anthropogenic disturbance, I recognize that anthropogenically-altered landscapes now dominate most of the planet (Vitousek et al. 1997, Ellis and Ramankutty 2008, Ellis 2011). Considering the ecological consequences of climate change in human-disturbed contexts may therefore offer practical insight with respect to land management and species conservation. The final study of my thesis takes place in two metropolises—Toronto and Ottawa, Canada.

Study organisms

Although more than 90% of the world's described bee species are solitary (Danforth et al. 2019), research and public attention have historically focused on social and domesticated species, particularly bumble bees and honey bees. Nevertheless, a growing number of studies have suggested that the contributions of wild solitary bees to pollination both in natural and agricultural systems can be significant, and in some contexts, even exceed those of social bees (Mallinger et al. 2019, MacInnis and Forrest 2019, Bänisch et al. 2021). If solitary bees have not received the scientific attention they merit, wasps have faced an even greater deficit (Sumner et al. 2018). Like bees, the majority (97%) of over 100,000 wasp species are solitary and all but a single subfamily are predators and parasites of arthropods (O'Neill 2001), many of which are phytophagous or considered to be pests of crop plants (Goulet and Huber 1993, Brock et al. 2021). Compared to other insectivorous animals (e.g., birds, mammals, amphibians), the contribution of wasps to arthropod population regulation is thought to be equal or even greater because their short generation times allow their populations to better match fluctuations in prey density (Archer 1985). Wasps feature in two of the four studies described in this thesis. The literature cited in my thesis will primarily represent studies on bees only because research on solitary wasps—whether on physiology, behaviour, natural history, population metrics, or geographic distributions—is woefully scarce. I hope this thesis will help to improve the paucity of knowledge when it comes to solitary wasps, even if only incrementally. (I have also included a few anecdotal notes for some taxa among the natural history observations in Appendix F.)

I focus primarily on a specific guild of solitary bees and wasps—those that nest in pre-existing cavities aboveground (hereafter “cavity-nesting bees and wasps”, or “wood-nesting bees and wasps” for chapter 3). This guild primarily includes species in the family Megachilidae for bees, and species in the Vespidae, Sphecidae, and Crabronidae families for wasps. Although most bee and wasp species are ground-nesting (Danforth et al. 2019), cavity-nesting species lend themselves particularly well to studies that require observing the insides of nests (or quantifying variables within them). Many cavity-nesting species readily occupy artificial nesting structures which can be placed in locations of interest, thereby eliminating the logistical challenge of finding nests in the field (as would be the case for ground-nesting species). Nests constructed in artificial structures can be easily opened to quantify variables such as brood cell production (reproductive output) and juvenile developmental success in addition to other potential variables of interest such as pollen usage and parasite attack (e.g. Farzan and Yang 2018, Spear et al. 2016, Forrest and Chisholm 2017).

Thesis outline

I begin in Chapter 1 by exploring the relationship between nesting timing and reproductive output in five species of solitary bees. I consider the contributions of seasonally varying environmental factors such as temperature and floral resource availability in shaping this relationship. In Chapter 2, I document the direct and indirect (floral-resource-mediated) effects of drought conditions on bee reproductive output. Chapter 3 evaluates the extent to which habitat quality, namely, the availability of nesting substrate, may limit future range shifts to higher elevations in cavity-nesting bees and wasps. Chapter 4 asks how developing cavity-nesting bees and wasps respond to variation in nest temperature in urban settings and quantifies the extent to which urban microhabitat features may buffer them from high background temperatures. In the General Discussion, I synthesize the findings of all four studies by discussing their combined implications with respect to the consequences of climate change for wild bees and wasps. I also discuss the limitations of my findings and identify areas requiring further research. I end in the Conclusion by highlighting the overall significance of this work.

Chapter 1

The earlier the better? Nesting timing and reproductive success in subalpine cavity-nesting bees

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The supplementary material associated with this chapter are in Appendix A.

Dr. Jessica Forrest introduced me to the research ideas for this study and together, we refined the overarching research goals and aims. This study involves the first six years of a 10-year dataset (2013–2023; excluding 2020) established by Dr. Forrest at seven sites in and around the Rocky Mountain Biological Laboratory which documents the nesting activity of cavity-nesting bees, hourly air temperature, and floral abundance. Dr. Forrest designed the field methods and led the data collection for this dataset every year of the study. Numerous students assisted with data collection over the course of the study period. Their names are listed in below. I assisted with data collection in the summers of 2017 and 2019 (although this study only uses data up until 2018). I wrote the code to analyze the data, generated figures, interpreted the results and drafted the manuscript with the guidance of Dr. Forrest.

The following individuals (in alphabetical order) contributed to data collection between 2013 and 2023: Abbie Hudson, Abi Zuber, Adam Groulx, Camille Roberge, Charlotte Cahill, Erin Francispillai, Gabriel Gauthier, Jessica Zung, Lena Heinrich, Madhupreeta Muralidhar, Mark Jin, Natasha Holy, Regan Cross, Sarah Chisholm, Sarah Silverman, Sophie Anderson, Vinko Culjak Mathieu

1.1 Abstract

Reproductive timing can affect an organism's production of offspring and its offspring's success, both of which contribute to its overall fitness. In seasonal environments, the timing of reproductive activity may be restricted to short periods of the year owing to numerous potential selective pressures such as variation in daylength, weather, food availability, predation, or competition. We documented the relationships between reproductive timing and individual reproductive success (total reproductive output and offspring success) in subalpine populations of five cavity-nesting solitary bee species. We also examined the relationships between bee reproductive success and environmental variables that are likely ultimate drivers of bee phenology in subalpine environments (i.e., seasonality of floral resource abundance and temperature). Over six years, we recorded solitary bee nesting timing, egg production, and offspring success using artificial nesting structures ("trap-nests") established at multiple study sites. We also quantified floral resources and recorded temperature throughout growing seasons. Bees nesting earlier in the season exhibited greater reproductive success. Reproductive output generally increased with floral abundance, although this relationship was weak and only significant for some bee species. Elevated temperatures were associated with increased nest construction rate, but not in greater reproductive output. These contrasting effects of temperature may have been driven by the negative relationship between temperature and bee longevity. Bees who nested for shorter durations of time (a proxy for longevity) produced fewer offspring, and individuals exhibiting the shortest nesting durations were also those that began nesting late in the season. Overall, bees who initiated nesting early and sustained activity for a long duration had the highest reproductive output. This work documents the relationship between reproductive phenology and fitness in wild insect populations and highlights the ways in which organisms can cope with the challenges of living in seasonal and highly variable environments.

1.2 Introduction

The timing of life-history events such as reproduction can affect offspring production and offspring success (Perrins 1970, Landa 1992, Varpe et al. 2007, English et al. 2018), both of which contribute to an individual's fitness. Numerous selective pressures can constrain reproductive timing such that there may be “optimal” temporal windows in which organisms maximize reproductive success. Resource abundance is likely the most well-documented constraint on timing, as reproducing individuals must meet both their own metabolic demands (which increase during reproduction), as well as those of their offspring (Varpe et al. 2007, Dunn et al. 2011, English et al. 2018); however, a number of other variables (abiotic and biotic) can also constrain reproductive timing. These include weather (Linton and Macdonald 2018), predation (Toyama et al. 2015), competition (Samplonius and Both 2019), daylength (Varpe and Fiksen 2010), lunar phases (English et al. 2018), and offspring developmental constraints (Frick et al. 2010). Individuals failing to time reproduction in accordance with favourable conditions given the abiotic and biotic constraints of their environments may experience decreased reproductive success.

The importance of reproductive timing is often accentuated in seasonal environments, as the time available for reproduction is constrained by short growing seasons (Perrins 1970, Varpe et al. 2007). Organisms may experience brief pulses of food abundance followed by periods of scarcity, suggesting that there should be selection for synchrony between reproductive activity and peak food abundance. Periods of favourable weather conditions for activities such as mating, nesting, rearing offspring, and foraging are also truncated in seasonal environments. Organisms may therefore need to time reproductive activity in accordance with seasonal weather patterns. Furthermore, for many organisms, offspring need time to undergo sufficient development prior to the end of the growing season (Roff 1980). Examples of this include ectotherms that must reach cold-tolerant life-stages before diapause (Tauber et al. 1986), mammals that must deposit sufficient fat stores before hibernation (Frick et al. 2010) and birds that must achieve a critical mass before migration (Braasch et al. 2009).

Reproducing early in the growing season could yield fitness costs or benefits. Early-season weather may be unpredictable and food may be scarce (Crecco and Savoy 1985, English et al. 2018); however, reproducing early can be advantageous, if offspring have more time to develop prior to the end of the season (Landa 1992) or if competitors and/or predators are scarce (Toyama et al. 2015). Individuals that reproduce early may also benefit from a longer reproductive period (Morrison et al. 2019). Late-reproducing individuals are likely to experience the opposite effects, with lower offspring mortality due to unpredictable early-season weather and potential resource scarcity, but also less time for offspring development. In seasonal environments, reproductive timing must reflect how organisms maximize

fitness while simultaneously constrained by numerous factors. Understanding the relationships among reproductive success, life-history timing, and the selective pressures constraining timing, is becoming increasingly critical as changes in climate alter the seasonal fitness landscape—including factors such as the phenology of vegetative growth and flowering, daily temperatures, and growing season length.

Here, we report a multi-year observational study on the reproductive timing of multiple subalpine solitary bee species. We address the following questions: (1) What are the consequences of nesting timing for (a) individual reproductive output and (b) offspring success? and (2) What are the relationships between bee reproductive success and the putative selective pressures of resource abundance and weather conditions? We expect positive relationships between local floral abundance and bee reproduction given that bees provision their offspring with floral pollen and nectar (Roulston and Goodell 2011). As such, bees whose nesting activity coincides with periods of greater resource abundance should have higher reproductive success. We also expect generally positive relationships between temperature and reproductive success given that foraging requires sufficiently elevated temperatures for efficient flight (Stone 1994, Polatto et al. 2014) and that thermal limitation may be especially acute in our subalpine study system where summers are brief and cool. Bees who nest during warmer periods of the growing season may therefore experience more opportunities for foraging, and therefore greater reproductive success. Finally, we also expect early nesting to be associated with increased offspring success because, all else being equal, it maximizes the time available for larval development. Overall, this study documents the fitness consequences of existing variation in life-history timing and explores the constraints that may drive those fitness consequences.

1.3 Methods

1.3.1 Study sites

Fieldwork was conducted from 2013 to 2018 in seven subalpine sites in the Rocky Mountains of Colorado, USA (38.9592°N 106.9897°W; 2900 m, Table S1. 1). Each year, data were collected from late-May or early-June until mid- to late-August. Each site contained 12–24 wooden “trap-nests” attached to tree trunks at a meadow edge. Trap-nests consisted of wooden blocks containing ten 14-cm deep holes of three diameters that attracted cavity-nesting insects. Holes were lined with paper straws allowing for nests to be temporarily removed and inspected (Figure S1. 1a & b).

1.3.2 Study organisms

We focused our study on the five most commonly observed cavity-nesting species found colonizing our trap-nests: *Osmia iridis* Cockerell & Titus, *O. coloradensis* Cresson, *O. montana* Cresson, *O. subaustralis* Cockerell, and *Hoplitis fulgida* Cresson (Anthophila: Megachilidae). All are solitary species that occur throughout western North America and nest in pre-existing cavities in woody substrate (Michener 2007, Wilson et al. 2010). In our study area, adult bees emerge between late-May and mid-June, although timings vary by species (Figure S1. 2). Following mating, females locate nesting cavities and construct nests consisting of a linear series of brood cells. Each brood cell contains a mass of pollen and nectar and a single egg (Figure S1. 1c). After progressing through several instars, larvae enter diapause for the winter before emerging as adults in the spring 1–2 years later (depending on the species and environmental conditions; Figure S1. 2). Hereafter, we refer to an individual’s nest as the entire contents of the nesting-straw they used, which typically contained multiple brood cells. Note that many individuals produced multiple nests each (i.e., used multiple straws; Figure S1. 1c).

1.3.3 Nesting timing, reproductive output & offspring success

To determine the consequences of bee nesting timing for individual reproductive output (Question 1a), trap-nests were visited periodically throughout the season to locate newly constructed nests and to monitor progress in existing nests. Site visits occurred every 4.1 ± 1.2 days (mean $\pm$ s.d.), except for one site which was inspected every 6.4 ± 2.6 days for logistical reasons (Table S1. 1). The dates on which we first observed females constructing a nest (hereafter “nest initiation day”) were recorded (or estimated if nest construction was initiated prior to site visits; see Data Analysis). Whenever possible, we caught and marked nesting females with unique colour combinations of paint on the mesosoma (Ullmann et al. 2016, Testors hobbyist’s paint: Vernon Hills, Illinois, USA; cf. Farzan and Yang 2018). Bees flew away and continued nesting after being marked. Females of all five species were marked in every year except for *H. fulgida* in 2013, 2014 and 2016. The paint marks allowed us to track individuals as they constructed successive nests (upon finding a new active nest at a site, we watched until the occupant made an appearance to determine her unique identity). To track nesting progress, nests were temporarily extracted from blocks, and the location of the most recently constructed pollen provision was marked on the outer surface of the straw each time sites were visited (Figure S1. 1b). Nests were always held horizontally and were only briefly extracted to minimize disturbance. Once females had completed and sealed nests, we counted the total number of brood cells (across all of the individual’s nests) to quantify an individual’s lifetime reproductive output (proxy for fitness).

We limited our investigation of the relationship between nesting timing and offspring success (Question 1b) to *H. fulgida* as it is the only uniformly univoltine species in our study (the other species are typically semivoltine at our sites; Figure S1. 2). Univoltinism in *H. fulgida* allowed us to assume that offspring failing to emerge the summer after nest construction had died and were not simply remaining in diapause for a second season. We used both larval development and emergence as measures of offspring success: measurements of developmental success (taken the same year eggs were laid; Figure S1. 2) allowed us to quantify offspring success independently of post-summer incidental mortality (e.g., trap-nest damage from snow or cattle) and to link the success of each individual offspring with the estimated date on which they were laid (hereafter “date laid”). Dates laid were interpolated based on our observations of nesting progress and the position of the brood cell within the linear series of eggs in a nest. We temporarily removed nests and cut small windows in the nesting-straws at every brood cell to determine if larvae had started constructing cocoons. Larvae that had initiated cocoon construction (evidenced by the presence of silk) were considered “successful” (Figure S1. 1d) and we assumed these individuals would survive winter. Larvae that had not initiated cocoon spinning, and brood cells that had been parasitized, or excavated by other insects, were considered “unsuccessful” (Figure S1. 1e). Straws were repaired with tape, reinserted into trap-nests, and left to overwinter. These data were recorded at two sites in 2017 and 2018 in the final days of our field season (between August 6 and 20) when most nesting activity had finished. While it is possible that some offspring initially recorded as “unsuccessful” eventually completed cocoon spinning after our last day of fieldwork, other work with *Osmia* spp. in our study system suggests that offspring born after August 1 (approximately) rarely survive the winter (Cahill et al. 2025).

We also quantified adult emergence in 2018 and 2019 as a second metric of offspring success to account for cases in which larvae completed cocoons after we measured development at the end of the previous field season. Emergence was also recorded for two nests constructed in 2014 (i.e., we recorded emergence from these nests in 2015), but cocoon completion data (larval development) were not collected from these two nests. We were unable to associate emerged offspring with their dates laid, and therefore analysed offspring success at the level of nests (straws) instead of individual offspring (see Data analysis). To determine emergence success, we attached transparent snap-cap vials to the front of occupied nest holes (Figure S1. 1f) in the spring following nest construction, as in (Forrest and Thomson 2011), and recorded the number of emerging insects from each nest.

1.3.4 Quantifying selective pressures

Floral resources

To quantify resources available to nesting bees throughout the season (Question 2), we surveyed floral host density in every year of the study when sites were checked for nesting. Published literature (Rust 1974), and examination of pollen samples from brood cells in trap-nests (Appendix A: Verifying floral hosts), showed that the five focal bee species provision their nests using different floral hosts: *Osmia iridis* are specialists on plants from the plant family Fabaceae, excluding *Lupinus* spp. (primary hosts at our study sites were *Lathyrus lanszwertii* (Kellog), and *Vicia americana* Muhl. Ex Willd.). *Osmia coloradensis*, *O. montana*, and *O. subaustralis* are specialists on plants in the Asteraceae family, and *Hoplitis fulgida* is a pollen generalist (details in Figure S1. 2). All plant taxa (typically individual species or genera, but sometimes groups of related genera with indistinguishable pollen; Table S1. 2) recorded to have been used for nest provisioning by our focal species and present at our sites were included in flower surveys. We quantified floral resources using the protocol of Forrest & Chisholm (2017). For days on which we did not conduct surveys, we interpolated floral density, by fitting a cubic spline with the R package “stats” (ver. 4.5.0.; R Core Team 2018) to the observed floral densities. This generated measures of floral density for each plant species on each day for all site-years.

Temperature

To determine the temperatures experienced by nesting bees, (Question 2), HOBO pendant temperature loggers (Onset Computer Corp., Bourne, Massachusetts, USA; accurate to ± 0.5 °C) were attached to the underside of one trap-nest at each site and provided hourly readings throughout the study. Because our study species forage only during the day, we used accumulated “degree-hours” between 8h00 and 20h00 with a 10 °C base as our metric of temperature instead of daily mean temperature. Although we do not know the exact activity temperature thresholds of our focal species, our field observations as well as studies of similar species suggest that a 10 °C base temperature is reasonable (Vicens and Bosch 2000, Forrest and Chisholm 2017). In our approach, one degree-hour accumulated whenever the hourly temperature was 1°C above the threshold temperature of 10 °C (e.g., an hourly temperature observation of 15 °C equals 5 degree-hours). We summed the daily degree-hours for each day and divided by 24 to produce degree-days.

1.3.5 Data analysis

We addressed our study questions (except Question 1b) using generalized additive mixed models (GAMMs; Wood, 2017) to facilitate the detection of nonlinear relationships between our predictor and

response variables. A summary of the models used to test each study question can be found in Table S1. 3. GAMMs were implemented using the “`gamm`” function in the “`mgcv`” package in R (Wood 2017). In all models, year and site were included as random effects. We used the “`gam.check`” function to test whether the number of basis functions for the smoothed fixed effects in our models were adequate, and to check assumptions of normality and homogeneity of variance. Because GAMMs do not generate single coefficients from which inferences can be made (i.e., positive or negative slope coefficients), we also ran linear mixed-effects models (LMMs; see supplementary methods in Appendix A) to obtain numerical values to support our visual assessments of GAMM fits and scatterplots. We focus primarily on GAMM results but refer to LMM results in Appendix A when necessary. We ran separate models for each bee species since floral hosts and nesting phenology differ interspecifically (Figure S1. 2); however, our interpretations focus on relationships that were consistent across most or all species.

For all multivariate models, we checked for concurvity among fixed effects using the “`concurvity`” function in the “`mgcv`” package. Concurvity describes the degree to which predictors are smooth curves of other predictors in the model (analogous to multicollinearity in linear models). Values are bound between 0 and 1, indicating zero and full concurvity respectively. Most pairwise indices were < 0.5 (mean = 0.27, s.d. = 0.14 for reproductive output models; mean = 0.28, s.d. = 0.17 for rate models), suggesting that concurvity was not severe in our models (values reported in Table S1. 8 & Table S1. 9).

1.3.5.1 Question 1: Consequences of nesting timing

1a: Reproductive output:

To test the consequences of nesting timing for individual reproductive output, we ran univariate GAMMs with nest initiation day as a smooth predictor for the total number of cells produced by each individually marked bee (individual reproductive output).

1b: Offspring success:

All analyses in which offspring success was the response variable (Table S1. 3) were conducted only with data on *H. fulgida* as we did not collect these data for the other four species. We tested for a relationship between date laid and larval success using a GLMM with binomial error. Date laid was rescaled to mean = 0 and standard deviation = 1. Cocoon success was scored as a binary response (1 and 0 for larvae that had and had not initiated cocoon-spinning by the end of the season, respectively).

We also tested the effects of nesting timing on the proportion of successful offspring in each nest. We conducted analyses at the level of nests (i.e., straws) and not individual mother bees as *H. fulgida* individuals were not marked in every year of our study (even though some individuals had multiple nests). We used a binomial-family GLMM with nest initiation day as a predictor for the proportion of cocooned offspring in each nest (total number of cocooned offspring divided by the total number of cells in the nest). This same model was repeated using the proportion of emerged bees in the following spring as the response. In both models, nest initiation day was rescaled (mean = 0; s.d. = 1) and the total number of cells in the nest was included as a weight. A Pearson correlation was used to verify that the proportion of cocooned and emerged offspring from the same nest were correlated.

1.3.5.2 Question 2: Relationship between reproduction & environmental variables:

To explore the relationship between environmental variables and bee reproductive success, we ran GAMMs with floral density and daily degree-days as smooth predictors of individual reproductive output. We included nest initiation day in these models to determine whether nesting timing continued to predict reproductive output after accounting for floral density and temperature. Floral density was summed across all host-plant taxa for each bee species and averaged over the inclusive number of days during which the individual was observed nesting (Appendix A: Floral density per individual). Degree-days were summed and averaged over the same period. We also analyzed the effects of floral density and temperature on bee nest construction rate (hereafter “nesting rate”). Nesting rate was calculated for each observation as the number of brood cells constructed since the previous site visit divided by the inclusive number of days elapsed between the current and previous site visits (hereafter “observation period”). Here, replicates were the observations of nests made at every site visit. We included day of year in these models as a covariate and individual nest identity as an additional random effect to account for the multiple observations per nest. Floral density was summed across all host-plant taxa and averaged over the inclusive number of days elapsed during the observation period. Degree-days were also summed and averaged over the observation period.

1.4 Results

Over six years, we observed and marked 208 *O. iridis*, 52 *O. coloradensis*, 71 *O. montana*, 66 *O. subaustralis*, and 48 *H. fulgida* individuals (445 individuals total). Collectively, these individuals constructed 3299 brood cells in 720 nests. An additional 341 cells in 128 nests were constructed by unmarked individuals. These were included in analyses of nesting rate but not in analyses of individual reproductive output as we could not confidently determine which nests belonged to which unmarked

individuals. Across all years, sites and species, successfully marked individuals represented at least 78% of all trap-nest occupants (based on the conservative assumption that each nest constructed by an unmarked bee belonged to a different unmarked individual). Details on the number of nests built by individuals of each species are in Figure S1. 3.

1.4.1 Question 1: Consequences of nesting timing

For all five bee species, individuals that initiated nesting early in the season produced significantly more brood cells over their lifetimes (Figure 1.1, Table S1. 5). We recorded cocoon completion (or lack thereof) for 203 *H. fulgida* larvae from 43 nests (18 nests in 2017, 25 in 2018). Of these, 153 had completed cocoons by late August. Larvae born later in the season were less likely to have initiated cocoon-spinning (Figure 1.2a; Z-score = -3.2; $p = 0.002$). Nests initiated earlier in the season had significantly higher proportions of offspring that had initiated cocoon spinning by the end of the season (Figure 1.2b; Z-score = -3.5, $p < 0.001$). Nests initiated earlier (in 2014, 2017 and 2018) also had generally higher proportions of emerged offspring (in 2015, 2018 and 2019 respectively), but this result was non-significant (Figure 1.2c; Z-score = -0.77, $p = 0.444$). The proportion of cocooned offspring in 2017 and 2018 was significantly correlated with the proportion of emerged offspring in 2018 and 2019 respectively (Figure S1. 4; $r = 0.54$, $df = 32$, $p = 0.001$).

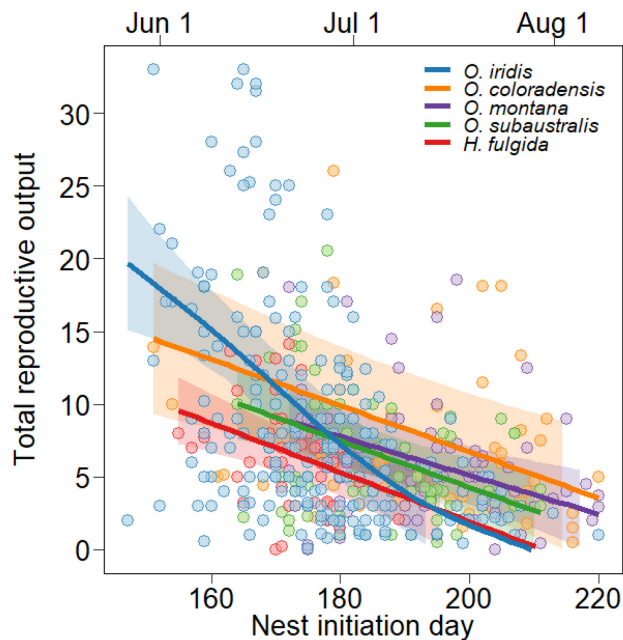


Figure 1.1. Bee reproductive output vs. nest initiation day.

Bee reproductive output as a function of nest initiation day for individual bees at seven study sites across six years. Lines are GAMM fits from a univariate model with year and site as random effects. Shading represents 95% confidence intervals of predicted fits. Sample sizes (n): *Osmia iridis*: n = 208, *O. coloradensis*: n = 52, *O. montana*: n = 71, *O. subaustralis*: n = 66, *H. fulgida*: n = 48.

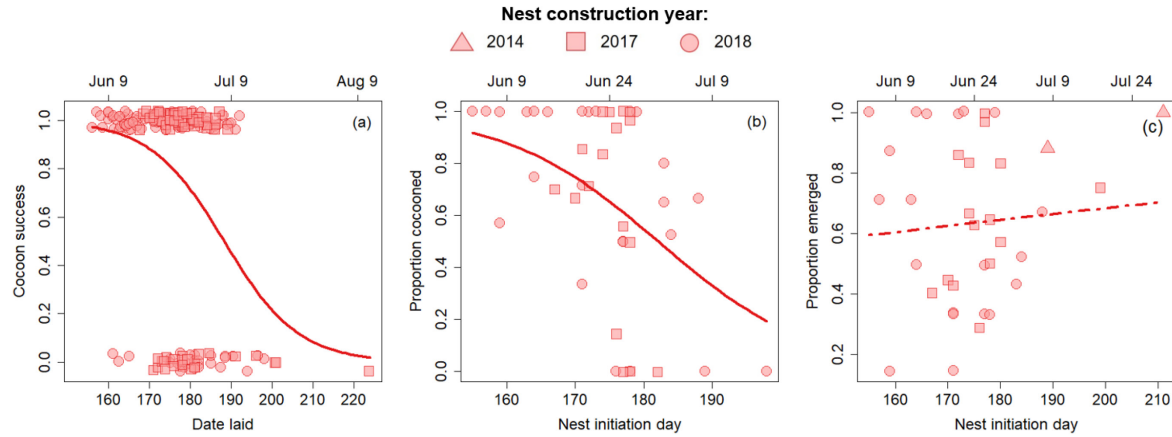


Figure 1.2. *Hoplitis fulgida* developmental success.

(a) Developmental success of *Hoplitis fulgida* larvae as a function of the day on which the egg was laid. Larvae that had initiated cocooning by the end of the season were considered “successful” (value = 1). $n = 203$ larvae over 2 years; $R^2_m = 0.18$. Curve is a binomial GLMM fit with site and nest identity as random effects. (b) Proportion of cocooned offspring as a function of nest initiation day. $n = 43$ nests over 2 years; $R^2_m = 0.14$. (c) Proportion of offspring successfully emerged vs. nest initiation day. $n = 39$ nests over 3 years; $R^2_m < 0.01$. Curves in (b) and (c) are binomial GLMM fits weighted by the total number of cells in the nest and with site as a random effect. Note that curves in this figure do not directly reflect the statistical results reported in the text, as those models included rescaled predictors and “year” as a fixed effect. Points are jittered in all panels. Significant ($p < 0.05$) and non-significant relationships are denoted by solid and dashed lines respectively.

1.4.2 Question 2: Relationship between reproduction & environmental variables

Seasonal patterns of floral host density varied among bee species (Figure 1.3a–c). Median first nesting day for *O. iridis* coincided relatively well with peak abundance of their floral hosts (Fabaceae), which occurred relatively early in the season. Median first nesting days for the three aster-specialist bees (*O. coloradensis*, *O. montana*, *O. subaustralis*) preceded peak Asteraceae flower abundance, which occurred later in the season, suggesting that approximately half the individuals observed in our study began nesting prior to floral peaks. Floral host density for *H. fulgida* was generally bimodal, exhibiting an early- and a late-season peak, with the relative magnitudes of early and late peaks varying across years and sites. Median first nesting day for *H. fulgida* coincided with the earlier of the two peaks. Daily degree-days peaked in mid- to late June before gradually declining (Figure 1.3d). Median first nesting day for all five bee species was roughly coincident with peaks in temperature (Figure 1.3d & Figure S1. 5).

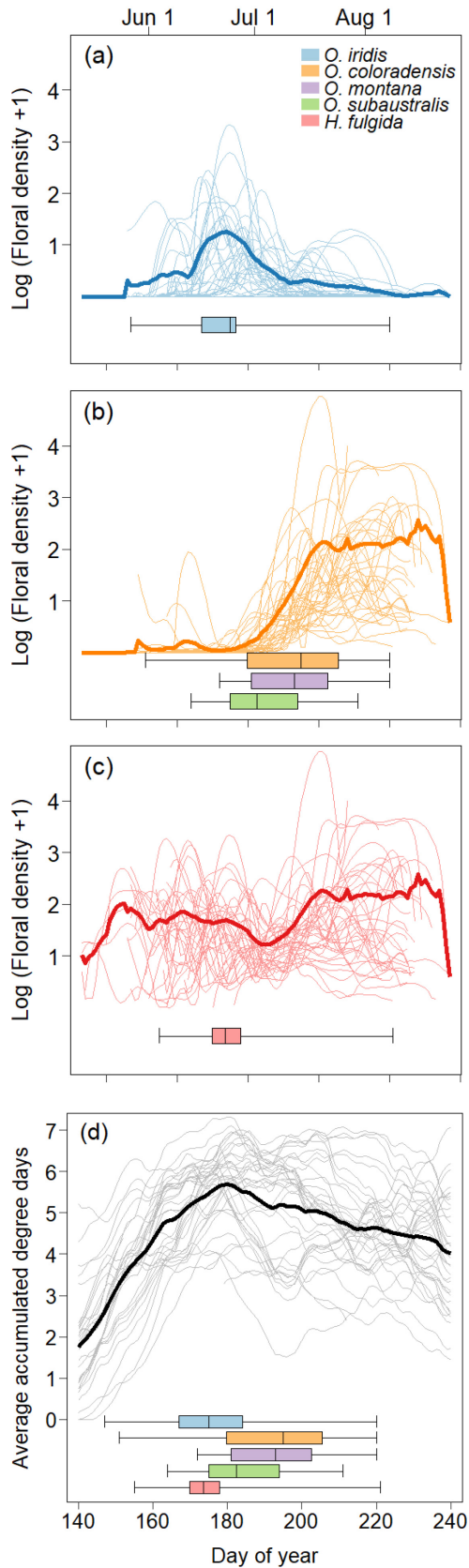


Figure 1.3. Seasonal patterns of floral density and temperature.

Floral density (log-transformed) for (a) floral hosts of *O. iridis*, (b) aster specialists, and (c) mix of taxa used by *H. fulgida* over the course of the season. Lines represent data collected over 6 years from 7 study sites for a total of 38 “site-year” combinations (some sites were not surveyed in every year). Each light line represents the total floral density (summed across all plant taxa for each flower guild) on a given day of the year, for a given site-year. Heavy lines represent floral density averaged across all site-years. (d) Average accumulated daily degree-days (above a threshold temperature of 10 °C) over the course of the season. Light lines represent values for each site-year. Heavy line represents the mean across all site-years. Lines for (d) show a 20-day moving average. Box-plots denote minimum, maximum, interquartile range, and median nest initiation day determined over all sites and years across all individuals of each bee species. Temperature curves in relation to bee nesting phenology plotted separately for each site-year for each species can be found in Figure S1. 5.

Nesting rate (brood cells per day) and reproductive output generally increased with increasing floral density (Figure 1.4a & c, Figure S1. 6), although these relationships were significant only for some species (Table 1.1 & Table S1. 5). Higher temperatures were associated with significantly higher nesting rates for most species (Figure 1.4b & Figure S1. 7; Table 1.1 & Table S1. 1). For *Osmia iridis*, nesting rate increased with temperature up to a certain point, before saturating when average daily accumulated degree-days exceeded 6 (equivalent to an average temperature of 21 °C between 8h00 and 20h00; Figure 1.4b). In contrast, relationships between temperature and total reproductive output were weak but generally negative for most species (Figure 1.4d; Table 1.1; primarily negative slope coefficients in Table S1. 5). For *Osmia iridis*, this relationship exhibited a hump-shaped pattern, with maximum reproductive output occurring at intermediate temperatures. Nest initiation day and day of year continued to be significant negative predictors of reproductive output and nesting rate respectively for all species after accounting for floral density and temperature (Table 1.1 & Table S1. 5).

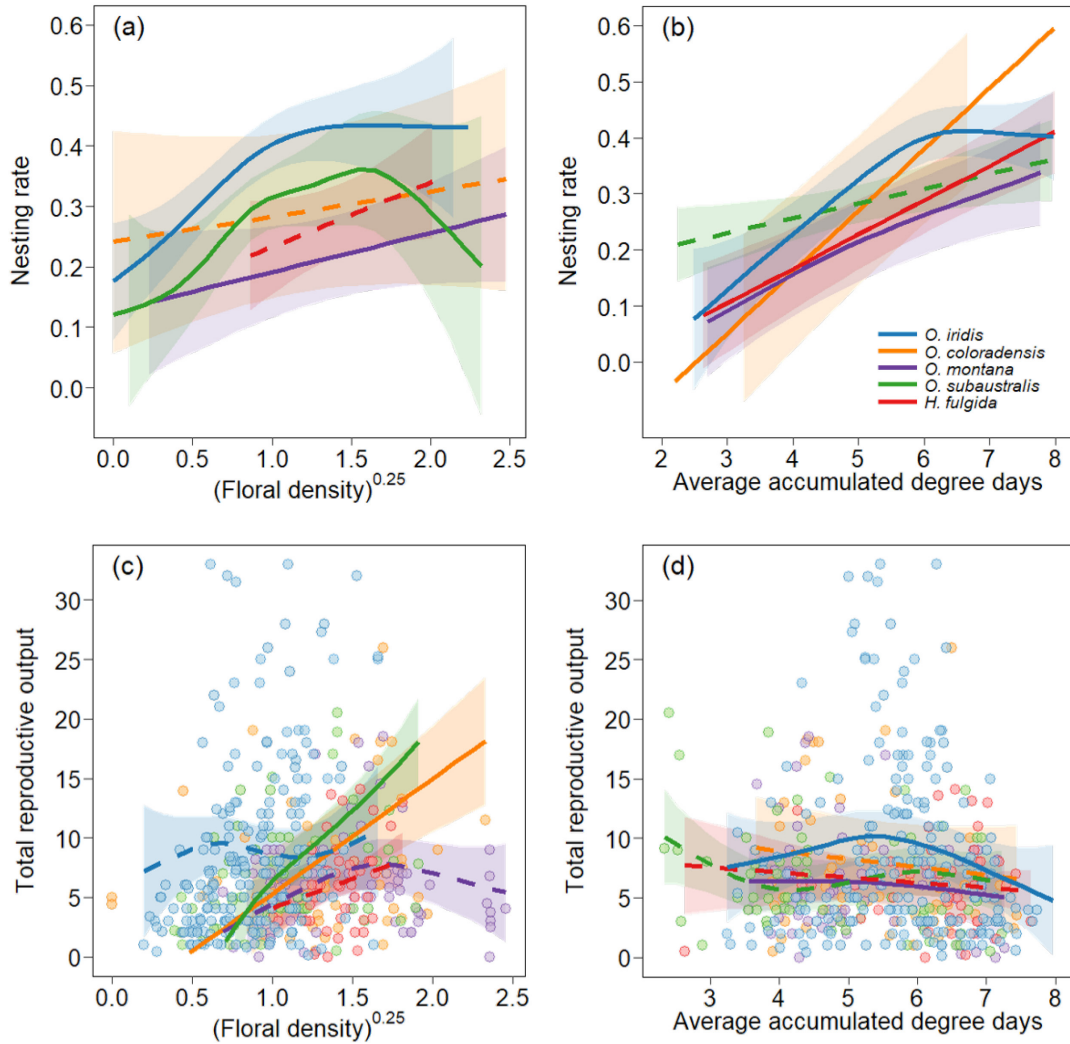


Figure 1.4. Bee nesting rate and reproductive output vs. floral abundance and temperature.

Bee nesting rate as a function of (a) floral density and (b) average daily accumulated degree-days. Each datapoint in these figures represents one observation of a nesting bee (with multiple observations per bee). Figures displaying individual datapoints can be found in Figure S1. 6 and Figure S1. 7. Bee reproductive output as a function of (c) average floral density and (d) average daily accumulated degree-days experienced by individually marked bees. An average of 3 and 8 average daily accumulated degree-days corresponds to average diurnal temperatures (8h00–20h00) of approximately 15 °C and 23.5 °C. Data are from seven study sites across six years. Lines are GAMM fits from multivariate models with year and site as random effects. Shading represents 95% confidence intervals of predictions. Lines are solid if the effect of the predictor is significant in multivariate models ($p < 0.05$) and dashed otherwise. Sample sizes for (a) and (b) are in Figure S1. 6 and Figure S1. 7. Sample sizes for (c) and (d) are as in Figure 1.1.

Table 1.1. Results of multivariate generalized additive mixed models.

Results of multivariate GAMMs with bee reproductive output and nesting rate as a function of nest initiation day (or day of year for rate), floral density, and temperature (average daily accumulated degree-days). Year and site were included as random effects. Bold indicates significant effects ($p < 0.05$). edf = estimated degrees of freedom, where 1 indicates a linear relationship, and greater numbers indicate increasing nonlinearity. R^2_{adj} = adjusted R^2 value for the full multivariate model.

Species	Response	Predictor	edf	<i>F</i>	<i>p</i>	R^2_{adj}
<i>O. iridis</i>	(Reproductive output) ^{0.5}	Nest initiation day	1	44.27	<0.001	0.32
		(Floral density) ^{0.25}	1	0.03	0.853	
		Temperature	2.89	3.88	0.011	
	(Nesting rate) ^{0.5}	Day of the year	1	42.65	<0.001	0.21
		(Floral density) ^{0.25}	3	9.89	<0.001	
		Temperature	3.54	20.83	<0.001	
<i>O. coloradensis</i>	(Reproductive output) ^{0.5}	Nest initiation day	1	48.60	<0.001	0.36
		(Floral density) ^{0.25}	1	24.57	<0.001	
		Temperature	2.30	1.35	0.387	
	(Nesting rate) ^{0.5}	Day of the year	3.26	5.14	0.001	0.06
		(Floral density) ^{0.25}	1	1.41	0.236	
		Temperature	2.47	24.10	<0.001	
<i>O. montana</i>	(Reproductive output) ^{0.5}	Nest initiation day	1	9.44	0.003	0.27
		(Floral density) ^{0.25}	2.27	2.19	0.120	
		Temperature	2.20	3.79	0.022	
	(Nesting rate) ^{0.5}	Day of the year	1	21.42	<0.001	0.056
		(Floral density) ^{0.25}	1	4.46	0.030	
		Temperature	2.65	5.59	<0.001	
<i>O. subaustralis</i>	(Reproductive output) ^{0.5}	Nest initiation day	1.80	79.57	<0.001	0.46
		(Floral density) ^{0.25}	3.62	31.83	<0.001	
		Temperature	3.06	1.64	0.204	
	(Nesting rate) ^{0.5}	Day of the year	3.77	3.47	0.019	0.099
		(Floral density) ^{0.25}	4.98	2.55	0.023	
		Temperature	1	3.10	0.080	
<i>H. fulgida</i>	(Reproductive output) ^{0.5}	Nest initiation day	1	8.46	0.006	0.21
		(Floral density) ^{0.25}	1	2.74	0.105	
		Temperature	1	0.28	0.597	
	(Nesting rate) ^{0.5}	Day of the year	1.27	15.69	<0.001	0.185
		(Floral density) ^{0.25}	1	1.26	0.262	
		Temperature	1	24.52	<0.001	

The difference between the temperature–nesting rate relationship (Figure 1.4b) and the temperature–reproductive output relationship (Figure 1.4d) contradicted our expectation that elevated temperatures, by increasing nesting rate, should increase reproductive output. However, while increased activity (to a certain extent) in warmer conditions has been widely documented in flying insects (Douwes 1976, Stone 1994, Hilfert-Ruppell 1998), the relationship between temperature and reproductive success may be more complex if elevated temperatures simultaneously impact fitness via other pathways. Specifically, warm temperatures can reduce insect longevity (Pearl 1928, Uçkan and Erginin 2003), an effect that could reduce reproductive output. To investigate this possibility post hoc, we added “nesting duration” (a proxy for longevity) to our models of reproductive output (along with floral density, temperature, and nest initiation day; Table S1. 3) to test whether accounting for longevity changed the relationship between these predictors and fitness. Nesting duration was calculated as the inclusive number of days between the first and last days on which we observed nesting activity for each individual bee.

As expected, nesting duration was strongly, positively associated with reproductive output for all species (Figure 1.5, Table 1.2, Table S1. 6). The relationship between reproductive output and nest initiation day remained negative with nesting duration accounted for (compare Figure 1.1 & Figure S1. 8 and see Table S1. 6). The inclusion of nesting duration also produced a significant positive relationship between reproductive output and floral density for 3 of 5 species (Table 1.2 & Table S1. 6) and resulted in generally positive (albeit mostly non-significant) relationships with temperature for four of five species (Figure 1.5). In other words, with bee longevity statistically accounted for, the effects of temperature were no longer negative (and even slightly positive).

To follow up on this finding, we conducted two additional post hoc tests using univariate models: We first directly tested the relationship between temperature and bee nesting duration (longevity) and found that nesting duration decreased significantly with increasing temperature for all species (Figure 1.6a; Table S1. 4 & Table S1. 7). Second, we tested the relationship between nest initiation day and nesting duration and found that bees that started nesting earlier also exhibited longer reproductive periods (Figure 1.6b; Table S1. 4 & Table S1. 7).

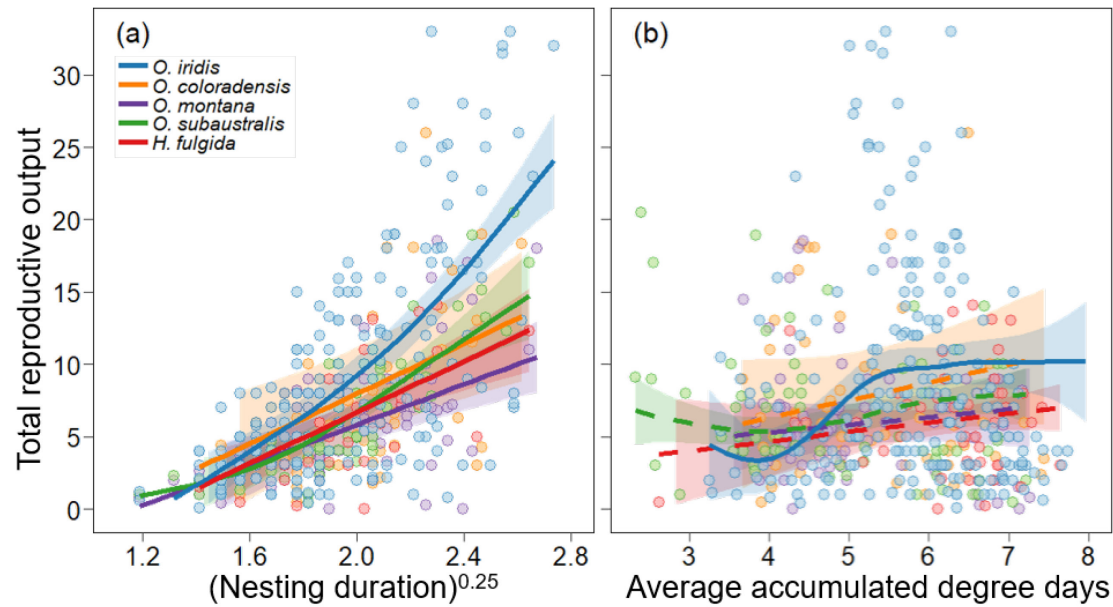


Figure 1.5. Bee reproductive output vs. longevity and temperature.

Bee reproductive output vs. (a) nesting duration (proxy for longevity) and (b) average daily accumulated degree-days after accounting for nesting duration. Lines are GAMM fits from post hoc multivariate models (Table 1.2) with year and site as random effects. Shading represents 95% confidence intervals of predictions. Lines are solid if the effect of the predictor is significant ($p < 0.05$) and dashed otherwise. Sample sizes as in Figure 1.1.

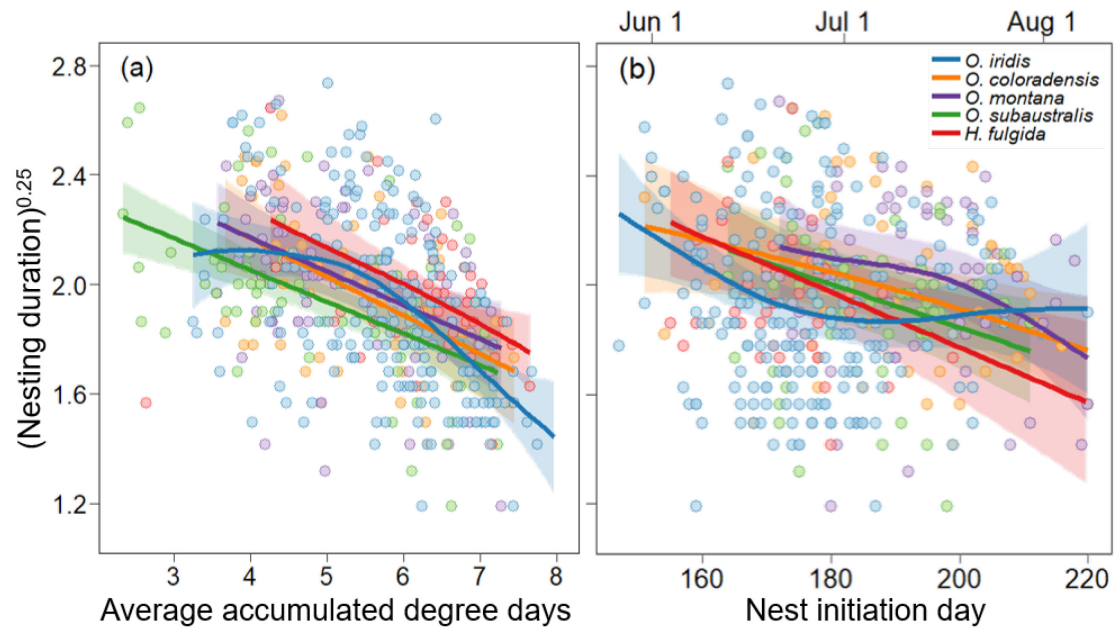


Figure 1.6. Bee longevity vs. temperature and nest initiation day.

Bee nesting duration (proxy for longevity) vs. (a) average accumulated daily degree-days and (b) nest initiation day for individually marked bees at seven study sites across six years. Lines are GAMM fits from univariate models (Table S1. 3) with year and site as random effects. Shading represents 95% confidence intervals of predictions. Sample sizes as in Figure 1.1.

Table 1.2. Post hoc multivariate generalized additive mixed model results.

Post hoc multivariate GAMM results for bee reproductive output as a function of nest initiation day, floral density, average daily accumulated degree-days, and nesting duration. Year and site included as random effects. Abbreviations and typography as in Table 1.1.

Species	Predictor	edf	<i>F</i>	<i>p</i>	R ² _{adj}
<i>O. iridis</i>	Nest initiation day	3.70	8.67	<0.001	0.70
	(Floral density) ^{0.25}	1	2.50	0.116	
	Temperature	3.74	9.39	<0.001	
	(Nesting duration)^{0.25}	1	233.17	<0.001	
<i>O. coloradensis</i>	Nest initiation day	2.17	6.75	0.002	0.35
	(Floral density)^{0.25}	1	9.06	0.004	
	Temperature	1	2.18	0.146	
	(Nesting duration)^{0.25}	1	10.72	0.002	
<i>O. montana</i>	Nest initiation day	1	1.56	0.217	0.36
	(Floral density) ^{0.25}	2.24	1.45	0.176	
	Temperature	1.91	1.17	0.353	
	(Nesting duration)^{0.25}	1	12.82	<0.001	
<i>O. subaustralis</i>	Nest initiation day	2.52	6.00	0.005	0.77
	(Floral density)^{0.25}	2.71	4.59	0.016	
	Temperature	2.13	2.36	0.127	
	(Nesting duration)^{0.25}	1	44.31	<0.001	
<i>H. fulgida</i>	Nest initiation day	1	0.72	0.402	0.39
	(Floral density)^{0.25}	1	4.49	0.040	
	Temperature	1	1.50	0.227	
	(Nesting duration)^{0.25}	1	14.56	<0.001	

1.5 Discussion

1.5.1 Early nesters exhibit higher reproductive success

Seasonal variation in reproductive success has been documented across many taxa (Landa 1992, Varpe et al. 2007, Frick et al. 2010, English et al. 2018, Morrison et al. 2019); however, the specific variables driving these patterns can vary substantially across species and environments. In our study area, bees who initiated nesting early in the season produced the most offspring (Figure 1.1). Our post hoc analyses showed that early nesting was strongly associated with increased longevity in bees; individuals that began nesting early experienced longer nesting durations (Figure 1.6b), and those that nested for longer, produced more

offspring (Figure 1.5a). This suggests that bee reproductive output could be limited by the amount of time individuals had to reproduce—a possibility given the short growing seasons they experience.

Although fecundity has been shown to come at the expense of longevity in many insects (Smith 1964, Tallamy and Denno 1982, Honda et al. 1998), we note that most of these studies take place in lab settings where extrinsic sources of mortality are few, and individuals receive controlled amounts of food. In these conditions, trade-offs in resource allocation between reproduction and longevity may be readily observed. In contrast, in field settings, extrinsic sources of mortality are numerous, and an individual's longevity can be influenced by many factors independent of resource allocation to reproduction, making longevity–fecundity trade-offs less detectable. We observed a strong positive relationship between longevity and reproductive output, possibly because constructing nests and provisioning each offspring requires time; individuals that initiate nesting early and that survive longest benefit from the most time to provision offspring. Positive longevity–fecundity relationships may also be especially pronounced in short-lived organisms living in seasonal environments as in our study system. Given that the snow-free period at our sites is brief and that female bees have a single nesting season lasting only a few weeks, there is likely little advantage to delaying reproduction in favour of extending longevity.

For *H. fulgida*, we also found that early-laid offspring were more likely to complete larval development by the end of summer, suggesting that they are more likely to successfully overwinter (Figure 1.2)—although this was not borne out in the emergence data. Bee larvae must progress through multiple instars, consume their pollen provisions, and spin cocoons—all of which can take several weeks (**Pitts-Singer and Cane 2011, Forrest et al. 2019**). As such, our results suggest that early nesters benefit from both increased total reproductive output and offspring success, likely because they experience more time for nest construction and offspring maturation. While we did not quantify offspring success for the four *Osmia* species in our study, we surmise that similar patterns would have been observed, given the time required for larvae to complete development (this has been quantified in lab settings), and based on field observations that eggs laid late in the season rarely survive in these species (**Cahill et al. 2025**). Notably, earlier lay dates for these semivoltine species can occasionally produce univoltine lifecycles which could be associated with fitness benefits beyond simply being able to complete development in time (**Forrest et al. 2019**).

1.5.2 Relationship between environmental variables and bee reproduction

Floral resources

Positive relationships between local floral resources and bee reproduction have been documented both in our subalpine study system (Forrest and Chisholm 2017) and in other settings (Roulston and Goodell 2011). In our study, relationships between floral resources and bee reproduction were generally positive, albeit surprisingly weak for some species and inconsistent across species (Figure 1.4a & c). All five bee species in our study also exhibited higher reproductive output early in the season regardless of when their floral hosts were most abundant (Figure 1.1 & Figure 1.3a–c). Taken together, these results suggest that while greater floral resource availability likely benefits bee reproduction, it may not be the primary constraint on nesting timing. The saturating relationship between floral density and nesting rate in *Osmia iridis* (the species represented by the greatest number of observations in our dataset; Figure 1.4a) seems to reinforce this possibility, as it suggests that increasing resource abundance is associated with greater reproductive output only to a certain extent. Physiological limits on egg production (Minckley et al. 1994) or the negative effect of other variables correlated with increasing local floral abundance (e.g., attraction of competing flower visitors) are possible explanations for this saturating relationship; however, due to the observational nature of our study, we are unable to identify a specific mechanism.

Moreover, given the brevity of the growing season in our study region, bees who begin nesting as soon as floral resources are even barely adequate may be most successful. Although individuals of some species that delay nest initiation may eventually experience improved resource conditions (i.e., increased floral abundance for aster specialists), this strategy is risky if later-season conditions end up being worse. Indeed, our study region often undergoes a mid-season decline in floral abundance prior to a late-season proliferation of Asteraceae flowers (Aldridge et al. 2011). If this late-season surge in floral resources failed to materialize (a possibility in drought years), late-nesting bees would have little time to compensate. Even if conditions for reproduction improved after a resource dearth, late-nesters would still be left with little time for nest construction and egg-laying. For the aster specialists, the apparent mismatch between nesting timing and flowering phenology could be interpreted as a bet-hedging strategy: although synchrony between nesting activity and peaks in flower abundance might have resulted in greater reproductive output, yearly variation in the timing and magnitudes of flowering peaks was also substantial (light lines in Figure 1.3b). As such, early nesting could be favoured because nesting too late could result in complete brood failure due to insufficient time for offspring maturation—a much greater cost compared to low resource availability early in the season. Determining whether bet-hedging is actually occurring in our study system

would require more information (Simons 2011); however, it is a conceivable strategy given the variability in abiotic and biotic conditions experienced by the bees in our study system.

We also note that the lack of a stronger and more consistent relationship between bee reproduction and floral resources could have arisen as an artefact of our study design. Study sites were located in meadows with relatively high floral abundance and it is possible that floral resources at our sites never declined sufficiently for bee reproduction to be noticeably compromised. It is also possible that our measurements of floral density did not adequately capture the variation in floral resources experienced by bees. Our flower counts assumed that all floral units were equivalent, despite interspecific differences in reward content and the possibility that the rewards in a counted flower were depleted by competitors. Regardless of the exact mechanisms at play, our results suggest that floral resources have less influence on the selective landscape of nesting timing than expected.

Temperature

Bees must maintain high thoracic temperatures in order to fly, and their foraging activity and efficiency generally increase with ambient temperature (Stone 1994). This was generally supported by our data (Figure 1.4b); however, these positive effects of temperature on nesting rate did not translate into increased reproductive output. Rather, the relationships between reproductive output and temperature appeared negative (albeit non-significant) for all species except *O. iridis*. The hump-shaped curve observed for *O. iridis* (incidentally the only species for which this relationship was significant) suggests that while moderate temperature increases were beneficial, temperatures above a certain point were detrimental. This is perhaps unsurprising given the well-documented asymmetrically unimodal responses of ectotherms to temperature gradients, often captured in thermal performance curves (Huey and Kingsolver 1989, Huey and Berrigan 2001).

Our post hoc analyses suggested that decreased reproductive output at higher temperatures could be linked to the effects of temperature on bee longevity. Elevated temperatures can increase an individual's metabolic rate, which can in turn increase oxidative damage, mutation rates, and overall "rate of living", leading to reduced longevity (Pearl 1928, Sohal 1986), and in the case of our study system, potentially less time to provision offspring. In addition to directly negatively impacting bee longevity and thus reproductive output, temperature could have also indirectly affected bee reproductive success, through effects on floral resources or natural enemies. At our study sites, parasite attack rates on *O. iridis* nests increase with temperature (Forrest and Chisholm 2017). That said, parasitism cannot explain the negative temperature–reproductive output relationships we observed, as our metric of reproductive output in this study includes all brood cells

produced by each individual and not only those that were unparasitized. Indirect effects of temperature could also be resource-mediated. Elevated temperatures can reduce flower abundance and/or reward production (Descamps et al. 2018, 2020); however, we see no indication of a negative relationship between floral density and temperature in our data (results not shown). Foraging activity of other pollinators other than our focal species may also increase in warmer conditions, possibly increasing competition for floral resources. However, given the inconsistent relationships between reproductive output and floral density we observed (Figure 1.4c), the negative relationships between temperature and reproductive output are likely not driven by floral resources.

We note that we have not explicitly tested whether temperature affects bee longevity, and that manipulative field experiments, perhaps in which bees are exposed to different temperatures in flight cages, may be required to identify the underlying processes at play; however, such studies are logistically difficult. Nevertheless, although we are unable to pinpoint exact mechanisms in our study, the negative association between temperature and bee longevity (Figure 1.6a), and the positive association between longevity and reproductive output (Figure 1.5a) were strong. Together, these results suggest that increasingly warm temperatures may not be beneficial despite the short-term benefits of increased nesting rate. With regards to nesting timing, it is therefore possible that early-nesters benefit from cooler early-season temperatures.

1.5.3 Additional determinants of lifetime reproductive success

Because our study is observational, we cannot segregate the effects of extrinsic and intrinsic factors on nesting timing and reproductive success. Here, we have addressed the roles of extrinsic factors specific to our study area (floral resources, temperature); however, the intrinsic qualities of reproducing females should not be ignored. Indeed, given that directional selection for early phenology is widespread across many taxonomic groups (Price et al. 1988, Olsson and Shine 1997, Varpe et al. 2007, Austen et al. 2017), there are likely general, non-taxon-specific processes at play. Specifically, females in better overall condition may be able to breed earlier and raise more offspring (Price et al. 1988). Early-reproducing individuals may therefore exhibit greater fecundity not because they reproduced early, but because they were in superior condition at the outset. As such, we are cautious in our interpretation of nesting early and continually producing brood throughout the season as a “reproductive strategy”. Rather, early nesting and long nesting duration may simply be manifestations of individual quality. Studies manipulating bee phenology are therefore useful complements to observational studies in disentangling the effects of correlated traits from the actual effects of nesting timing (Farzan and Yang 2018). We also note that while the patterns we

observed are consistent with directional selection for early nesting, we do not know whether nesting timing in our focal populations is heritable (determining this would likely require selection experiments). As such, while we may have observed selection for early nesting, we cannot determine whether this selection will yield an evolutionary response.

1.5.4 Implications for a changing climate

Climate change has been linked to earlier seasonal activity in numerous organisms (Ge et al. 2015, Asch 2015, Bourret et al. 2015). In our study region, flowering phenology has advanced in recent decades (CaraDonna et al. 2014); whether there have been parallel shifts in bee phenology is unclear. We have so far assumed that the bee traits observed in our study are adaptive in the current selective landscape—that is, the observed timing of bee nesting is adaptive given the seasonal patterns of floral abundance and temperature we observed over our six-year study. This may not be true, as temperature and flowering conditions may have shifted independently of bee nesting phenology before our study began. This could in principle explain the apparent selection for earlier nesting observed in our study—although, as aforementioned, the relatively inconsistent associations between reproductive output and floral abundance (Figure 1.4c), as well as our observation that the aster specialists already initiate nesting before peaks in flower abundance (Figure 1.3b), suggest this is unlikely. Moreover, because the association between early phenology and high reproductive output is so widely documented across many taxa, selection for early reproduction may not require the invocation of climate change.

Regardless, one might expect that climate-driven advances in bee phenology will improve bee reproductive success since early-nesting bees exhibited the highest reproductive output. Female bees may indeed benefit from longer growing seasons, which could relax the time constraints on bee reproduction and larval development (Buckley et al. 2015). While this positive effect of advancing phenology is superficially plausible, other covarying factors might be harmful. For example, earlier spring snowmelt is also associated with increased frost-damage to flower buds of some plant species in our study region (Inouye 2008). Bees active early in the season might therefore experience resource shortages. Also, given the generally negative effect of temperature on bee longevity and reproductive output, the increasing summer temperatures typically following an early spring might negate the positive effects of a longer season. For these reasons, while our study demonstrates the benefits of nesting early in the season, we do not suggest that *increasingly* earlier nesting will have favourable outcomes.

1.6 Conclusion

Overall, these results demonstrate that in our subalpine study system, bees that nest early experience the greatest reproductive success. We suggest increased time for larval development, short season lengths constraining the time bees have to provision nests, and cooler early-season temperatures as possible explanations for this pattern (although underlying mechanisms have yet to be tested experimentally). Given the brevity of the growing season in our study region, the benefits of nesting early and sustaining activity for a long period likely outweigh the benefits of reproductive synchrony with peak resource conditions. While this seemingly contradicts the findings of phenology studies which emphasize the importance of synchrony between bees and flowers (Schenk et al. 2018a, Kudo and Cooper 2019), our results highlight the ways in which organisms cope with the challenges of living in a highly seasonal environment.

1.7 Acknowledgements

We thank the RMBL and particularly Jennie Reithel for access to study sites. We thank all field assistants for their contributions in building the multi-year dataset, members of the Forrest lab for valuable discussion, Michael Stemkovski for advice on using general additive models, and two anonymous reviewers for their insightful comments.

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Chapter 2

Up high, hot and dry: individual reproductive output in subalpine bees declines with increasing drought severity

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The supplementary material associated with this chapter are in Appendix B.

Dr. Jessica Forrest introduced me to the research ideas for this study and together, we refined the overarching research goals and aims. This study involves nine out of ten years of data from the same long-term dataset used in Chapter 1 (2013–2023; excluding 2020) established by Dr. Forrest (see Chapter contributions for Chapter 1). For this chapter, we collaborated with Dr. Brian Inouye, who is currently the lead investigator of a 45-year-long flowering phenology and abundance dataset at the RMBL first initiated by Dr. David Inouye and his colleagues in 1973. Many scientists, students, and technicians contributed to this dataset, which is described in <https://osf.io/jt4n5/overview>. I incorporated a subset of this long-term dataset along with a parallel dataset containing long-term climate data for the RMBL area compiled by Dr. Rebecca Prather, published in Ecology (Prather, R. M., Underwood, N., Dalton, R. M., Barr, B., & Inouye, B. D. (2023). Climate data from the Rocky Mountain Biological Laboratory (1975–2022). *Ecology*, 104(11), e4153.). The climate data are derived from several sources including local weather stations data acquired through the National Oceanic and Atmospheric Administration as well as an on-site weather station at the RMBL maintained by weather expert billy barr. I wrote the code to analyze the data, generated figures, interpreted the data and drafted the manuscript with the guidance of Dr. Forrest and in collaboration with Dr. B. Inouye.

2.1 Abstract

Wild bees play indispensable ecological roles in many ecosystems, yet declines in many species have been documented in recent years. These declines have been linked to numerous anthropogenic pressures, including climate change, which can influence bee populations directly (i.e., through effects on individual physiology) and indirectly (e.g., through changes to floral resource quantity and quality). Widespread changes in the distributions and abundances of many bee species have been linked to climate change at large spatial scales; yet the local-scale processes that generate these broad-scale patterns are little known. Specifically, it is unclear how climate change influences the fitness of individual bees, despite the fact that broad-scale patterns of decline must be driven by individual-level processes. Our study examines the individual fitness responses (i.e., reproductive output) of five solitary bee species in the genus *Osmia* to variation in local climate variables in subalpine habitats. Over nine years, we tracked brood cell production in over 700 individual female bees, conducted repeated surveys of floral abundance (while taking into account the specific floral host taxa used by each bee species), and recorded local precipitation and temperature at seven sites. Our data revealed both direct and indirect (floral resource-mediated) negative effects of drought: the total number of brood cells produced by nesting females decreased significantly in summers characterized by greater drought severity and high temperatures—a relationship driven partly by significant decreases in floral host-plant availability in hotter and drier years. Our study highlights how the negative consequences of climate change for bee populations can manifest at the level of individuals and the role of floral resources in mediating these relationships. Overall, our results suggest that the increasingly warm and dry conditions forecasted for our study area will have net negative effects on the demographic success of these solitary bees.

2.2 Introduction

The consequences of climate change for biodiversity are becoming increasingly apparent (Scheffers et al. 2016, Pörtner et al. 2021). A growing number of studies have documented widespread population decline in many taxonomic groups in response to rising temperatures and increased frequency and intensity of climate extremes (Lister and Garcia 2018, Spooner et al. 2018). Many of these studies have taken a broad-scale approach, documenting changes in the distributions, ranges, and extinction risks of many species in aggregate across large spatial scales. While their findings have helped to quantify the overall rate and magnitude of biodiversity decline due to climate change, the mechanisms driving the observed patterns remain difficult to decipher. Ultimately, broad-scale patterns of biodiversity loss due to climate change represent the cumulative response of individuals within populations to changes in their local climate conditions. Understanding the processes that drive the consequences of climate change for biodiversity requires empirical studies at local scales that document relationships between climate variables and individual fitness, all while considering the idiosyncrasies of species, populations, and their habitats.

Studies that quantify metrics of lifetime individual fitness in natural animal populations are relatively rare (Clutton-Brock and Sheldon 2010, Sheldon et al. 2022). Individuals within a population must be caught, identified, and continuously tracked throughout their lifetimes—requirements that may be impractical or even impossible for many animals, especially those that have long lifespans and for which access to sufficiently high densities of recognisable individuals is limited. Quantifying climate predictors such as temperature and moisture in ways that meaningfully capture the conditions directly experienced by individuals may pose an additional challenge, especially for animals that are migratory or for those that have unknown or large home ranges. Moreover, in addition to the direct (i.e., physiological) impacts of climate, individual fitness can be influenced by climate indirectly through its effects on extrinsic variables such as resource abundance, habitat suitability, and interspecific interactions. Capturing the net effects of climate change for individual fitness would therefore require that these indirect climate pathways be considered along with direct physiological effects. Nevertheless, challenges may arise in quantifying indirect pathways if we lack knowledge of the organism's natural history traits, e.g., their dietary preferences, lifecycles, habitat requirements, interactions with mutualists, competitors, predators, and pathogens. Overall, studies that consider both direct and indirect pathways between climate and individual fitness may be critical for understanding the processes underlying large-scale biodiversity decline yet are rare due to the practical challenges associated with gathering individual-level data in natural populations and inadequate natural history knowledge for many species.

Solitary bees are ideal candidates for studying the effects of climate on individual fitness. Each female solitary bee constructs her own nests and performs tasks such as provisioning offspring and defending the nest from parasites and predators over a single breeding season that typically lasts only for a few weeks (Danforth et al. 2019). Most species are small-bodied, central-place foragers (females build nests in fixed locations) with flight ranges spanning no more than a few hundred metres (Greenleaf et al. 2007, Zurbuchen et al. 2010). Species-specific natural history traits such as dietary and nesting resource requirements are also relatively easy to observe for most species, facilitating the incorporation of these variables into study designs (Dorian et al. 2024). These traits alleviate some of the challenges frequently associated with quantifying individual fitness in natural populations. Over seventy-five percent of the 20,000 globally described bee species are solitary, and despite their important contributions as pollinators in both natural and agricultural systems, they receive little attention relative to social bees such as honey bees and bumble bees (Danforth et al. 2019).

Over recent years, climate change has been linked to broad-scale declines in both social and solitary bee species, although most studies have focused on the former (Kerr et al. 2015, Kammerer et al. 2021, Jackson et al. 2022). Substantial variation in the direction and magnitude of the responses of bees to climate change has also been documented, with populations of some species remaining stable, and others even showing positive trends (Powney et al. 2019, Kammerer et al. 2021, Kazenel et al. 2024). This variation may in part be attributable to the fact that bees inhabit highly diverse environments and exhibit widely divergent natural history traits (e.g., degrees of sociality, pollen specialization, nesting habits, lifecycles, body sizes; Michener 2007). Studies that aim to understand the processes driving relationships between bees and climate may therefore benefit from a focused approach with fewer species and a careful consideration of their natural history traits. For the most part, the processes that underpin the responses of bees to climate change remain unknown, despite the fact that this information may be necessary for predicting the responses of species to future environmental change (but see Kazenel et al. 2024).

We conducted a nine-year field study in which we documented the relationships between seasonal weather variables (drought severity, precipitation, temperature) and individual reproductive output in natural populations of five species of wild solitary bees in the genus *Osmia*. We also considered the pollen requirements of each species by quantifying local floral resource abundance based on the floral host usage of each species and examined the potential indirect, resource-mediated relationships between climate and bee fitness. Our study took place in subalpine meadows in the Rocky Mountains of Colorado in an area that has experienced relatively little anthropogenic land-use change, allowing for the effects of changing climate conditions on bee populations to be investigated independently of other potential

stressors (e.g., urbanization, pollution, pesticides). The state of Colorado and much of southwestern North America is highly drought-prone and predicted to sustain increasingly severe climatic changes including reduced snowpack, earlier snow melt, heat waves, and reduced summer rainfall (Rhoades et al. 2018, Wahl et al. 2022). Many of these changes have already manifested. Montane species may be especially vulnerable to rising temperatures as rates of warming may be amplified at high elevations (Trew and Maclean 2021). At the same time, positive effects of drought for high-elevation species are also conceivable. For example, warmer temperatures and reduced rainfall events may benefit bees and other fair-weather foragers by increasing favourable foraging opportunities—which may be especially limited in our study area given the brevity of the season, the generally cool temperatures, and frequent summer storms. Overall, the demographic effects of drought on many organisms in the region remain unclear.

2.3 Methods

2.3.1 Study sites

Data were collected every year from 2013 to 2022 (except 2020 due to COVID-19 travel restrictions) in seven subalpine sites around the Rocky Mountain Biological Laboratory (RMBL), Colorado, USA (38.9592°N 106.9897°W; 2900 m; Figure 2.1a). Sites span an elevational gradient of approximately 700 m, from 2729 to 3440 m. Not all sites were monitored in every year of the study (Table S2. 1). In each year, data were collected starting late May or early June until mid- to late August. Sites contained 12–24 wooden trap-nests attached to the trunks of dead or dying trees located at a meadow edge. Trap-nests consisted of wooden blocks containing ten 14-cm deep holes of three diameters (4.5, 6.1 and 8.2 mm) that attracted cavity-nesting Hymenoptera (bees and wasps). Holes were lined with semitransparent paper straws allowing for nests to be temporarily removed and for the number of brood cells contained in them to be counted without disturbing actively nesting females (Figure 2.1b & c).

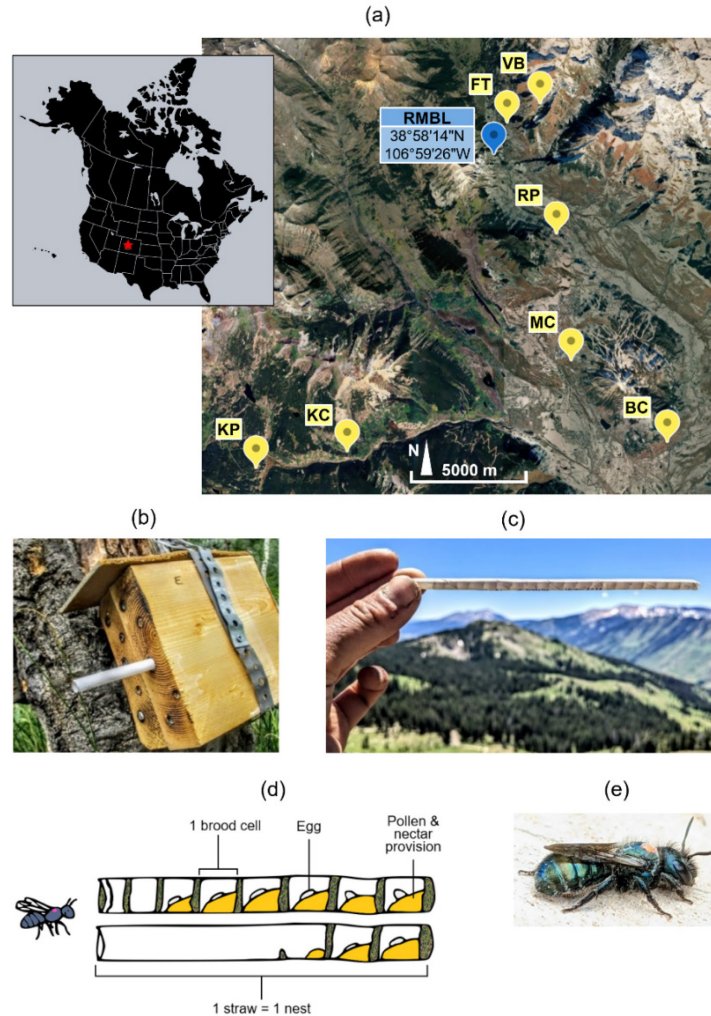


Figure 2.1. Site locations and study design.

(a) Location of the seven study sites (yellow markers) where bee brood cell production and flower data were collected between 2013 and 2022 and the RMBL (long-term study site; blue marker) where flower data were collected from 1976–2022. See Table S2. 1 for site details and abbreviations. (b) Wooden trap-nest attached to tree with one paper nesting-straw partially extracted. Cavities are of three diameters: 4.5, 6.1, and 8.2 mm. (c) Paper straw containing an *O. tristella* nest. Brood cells are visible and can be counted when the straw is held up against the light. This nest contains approximately 20 brood cells. (d) Diagram of nest interiors with an individual bee (marked with pink paint) who has two nests, i.e., she has so far used two paper straws throughout her nesting period. Nests consist of a linear series of brood cells each of which contains an egg and pollen-and-nectar provision. We counted the number of eggs produced by each individual across all their nests to determine total individual lifetime reproductive output. In this illustration, the upper nest is complete (it has an outer seal in addition to the outermost brood cell wall), while the lower nest is still in progress. In the field, this individual's reproductive output would have been scored as a decimal value (e.g., ~8.3 - 8.4 brood cells) given the partially complete brood cell in her second nest and lack of egg. If no additional progress were to be made in this nest by the end of the season, this individual's reproductive output would have been rounded down to 8 in statistical models. (e) *O. tristella* female marked with dot of orange paint on mesosoma. Photo & illustration credit: L.H.W.

2.3.2 Study organisms

Numerous cavity-nesting bee species have been recorded nesting in the trap-nests at our sites (Forrest and Thomson 2011); however, the total brood cell production of individual females was only consistently recorded for a subset of species—primarily those that were relatively common at the sites and for which brood cells were not concealed in nesting material (i.e., some *Megachile* spp.). We selected the five most well-represented species across sites and years: *Osmia coloradensis* Cresson, *O. iridis* Cockerell and Titus, *O. montana* Cresson, *O. subaustralis* Cockerell, and *O. tristella* Cockerell. All are solitary bee species that occur throughout western North America and nest in pre-existing cavities in wood (Michener 2007, Wilson et al. 2010). In our study area, adult bees typically emerge between late May and mid-June, the specific timing varying by species and site (Wong and Forrest 2021). Individuals mate, and females locate nesting cavities and construct nests. Nests consist of linear series of brood cells with each cell containing a mass of pollen and nectar along with a single egg (Figure 2.1d). A female bee may construct multiple nests, almost always sequentially, over her lifetime. Upon hatching, larvae progress through several instars over the course of the summer before entering diapause for the winter. All five species are typically semivoltine in our study area, emerging as adults two years later although one-year lifecycles are observed occasionally (Forrest et al. 2019).

2.3.3 Bee reproductive output

Most sites were visited every 3–5 days (Table S2. 1). During each site visit, we checked trap-nests for nesting activity by temporarily extracting the paper straws and inspecting their contents. Upon identifying a new active nest at a site, we watched the nest entrance until the nest owner (nesting female) appeared. Females were then caught and marked with unique colour combinations of non-toxic paint (Testors hobbyist's paint: Vernon Hills, Illinois, USA; Figure 2.1e). The paint marks allowed us to track individual bees as they constructed successive nests because approximately a third of all individuals built more than one, i.e., used multiple paper straws (Figure 2.1d). Females were released after being marked and continued nesting. Once nests were completed and sealed, we quantified each female's reproductive output by summing the total number of brood cells they had produced across all their nests. Although this study design does not account for brood cells constructed outside of the trap-nests in naturally-occurring cavities at our sites (if any), females who built multiple nests typically began nesting in a new hole within the same trap-nest immediately after completing the first. Species identifications of nesting individuals were ascertained using a combination of species-identifying morphological features visible in the field (some features are documented in Appendix F), as well as nest pollen contents (see “Floral resources” below). Further details on trap-nest monitoring protocols are in Wong & Forrest (2021).

2.3.4 Floral resources

We quantified floral resources following the protocol of Forrest & Chisholm (2017). These data were used to characterize the relationship between climate variables and the floral resources available to nesting bees, as well as the relationship between floral resources and bee reproductive output. Floral surveys were conducted during every site visit the first seven years of the study (every 3–5 days; 2013–2019) and weekly in 2021 and 2022. The first flowering of some taxa was missed at some sites in 2013 as floral surveys were initiated only when bees started nesting that year. During surveys, we counted open flowers only of plant taxa identified as potential pollen sources for our focal bee species (floral hosts) since four of the five species were pollen specialists: *Osmia coloradensis*, *O. montana* and *O. subaustralis* are specialists on plants in the Asteraceae family (Rust 1974); *O. iridis* are specialists on plants from the tribe Fabeae or possibly the broader “IRLC” clade of papilionoid legumes (Fabaceae; at our sites, these were primarily *Lathyrus lanszwertii* Kellogg and *Vicia americana* Muhl. Ex Willd. (The Legume Phylogeny Working Group 2013). *Osmia tristella* are pollen generalists (Rivest et al. 2024). Floral hosts were determined based on past work in our study system and previously published work from other studies (Spear et al. 2016, Wong and Forrest 2021, Forrest 2024). All plant taxa (typically species or genera, sometimes groups of related genera with indistinguishable pollen) found in pollen samples and present at our sites were included in surveys. Taxa that were identified as floral hosts part way through the study and missed in earlier years were included in all subsequent surveys; we ascertained that their contribution to our metrics of floral resources did not qualitatively influence our results. See Forrest (2024) for details on plant taxa. Hereafter, “floral group” refers to all floral hosts used by each bee species; these include Asteraceae (*O. coloradensis*, *O. montana*, *O. subaustralis*), tribe Fabeae (*O. iridis*), and generalist hosts (*O. tristella*; Table S2. 2).

In addition to conducting floral surveys at our study sites, we accessed two multidecadal datasets from the RMBL to further examine the relationship between climate variables and floral resource abundance. The RMBL is located within 15 km of all our study sites (Table S2. 1); climate conditions, floral species composition, and phenology are therefore similar. The first dataset contained floral abundance and phenology records of 45 of the 49 plant species we surveyed (missing taxa represented 10% of the floral hosts of the generalist bee species in our study, *O. tristella*). Counts of these species from this dataset were combined according to the three floral groups. Briefly, each year from 1976 to 2022 (except 1978 and 1990), all open flowers in twenty-one 2 × 2 m plots were counted every 2–3 days throughout the growing season. Surveys generally occurred from May to September. Methodological details and

metadata are in Inouye (2008) and Inouye et al. (2022). The second dataset contained long-term weather data amalgamated from several local sources with the same temporal coverage as the long-term floral abundance dataset (Prather et al. 2023). Although these data do not perfectly represent the flower and climate conditions experienced by the bees at our sites, we incorporated them in our study as they allow for the floral resource–climate relationship to be examined over a timeframe that captures greater climate variation than our nine-year dataset.

2.3.5 Climate variables

At each of the seven sites, an unshielded HOBO temperature logger (Onset Computer Corp., Bourne, Massachusetts, USA; accurate to ± 0.5 °C) was attached beneath one centrally-located trap-nest and provided hourly readings throughout the entire duration of the study (additional details in Appendix B). Because we did not have in-situ measures of precipitation at the seven sites, we acquired daily precipitation for each site and year using the parameter-elevation regressions on independent slopes model (4 km spatial resolution; PRISM Group, Oregon State University, accessed February 8, 2024). These data were used to generate metrics of precipitation and temperature, and to calculate a drought index that combines precipitation and temperature, which were our predictor variables (models described below).

We used the Standardized Precipitation Evapotranspiration Index (SPEI) to quantify drought severity as it includes both precipitation and temperature and can be quantified at varying temporal grains and windows, i.e., indices can be calculated over durations of time relevant to a particular organism and with respect to varying calendar dates (Vicente-Serrano et al. 2010). For example, a 3-month SPEI ending in October characterizes conditions averaged over the months of August through October. SPEI is a normalized index; values of zero indicate no change relative to historical values. We used negative SPEI values ($-1 * \text{SPEI}$) in our models and figures to make results more intuitive to interpret and visualize; large positive values indicate severe drought, and large negative values indicate cool and wet conditions. The Hargreaves method was used to calculate monthly potential evapotranspiration (Beguería et al. 2014). All SPEI values were calculated using the R package “SPEI” (Beguería and Vicente-Serrano 2023). Hereafter, we refer to (negative) SPEI as “drought severity”.

2.3.6 Data analysis

General approach

We used linear models to examine relationships between climate variables and two response variables: (1) floral density and (2) total brood cell production (individual lifetime reproductive output). For each response variable, we ran two models—one with drought severity as the sole climate predictor (hereafter “drought severity model”) and a second with temperature, precipitation and their interaction as predictors (hereafter “component variable model”). The goal of the drought severity models was to test the consequences of the specific combination of climate variables associated with drought (i.e., high temperatures, low precipitation), while the component variable model aimed to delineate potentially more nuanced relationships between our response variables and temperature and precipitation. The temporal coverage of drought severity, temperature and precipitation varied depending on the response variable in the model. Models are described in detail below and a list of all final models is in Table S1. 3.

All analyses were conducted in R (version 4.4.1; R Core Team, 2024). For all models, we examined pairwise correlations between continuous predictor variables and calculated Variance Inflation Factors (VIFs) using the “check_collinearity” function in the package “performance” (Lüdtke et al. 2021), and the “vif” function in base R. Variance Inflation Factors and correlations between predictor variables were generally low (Figure S2. 8 & Figure S2. 9; maximum VIF = 2.23). Models where predictors were strongly correlated, and where we suspected multicollinearity may have influenced our findings, are noted in the results. Homoscedasticity was assessed by visually inspecting residual plots; data were transformed in cases where plots indicated model heteroscedasticity (transformations specified below).

Floral density models

For both datasets, we only included floral counts between June 7 and August 16 because these dates correspond to the latest start date and earliest end survey date over the duration of trap-nest monitoring at our seven study sites was calculated over a modified “water year” (September 1 of the previous year to August 31 of the current year; same temporal coverage as drought severity). Mean temperature was averaged over a four-month period from May to August (hereafter “summer”), reflecting the period during which most species flower. Hereafter, we refer to these climate metrics as “water-year drought-severity”, “water-year precipitation” and “summer temperature”. Precipitation and temperature were scaled and centred to mean = 0 and standard deviation = 1.

For the flower data collected at the seven study sites, we used maximum floral density observed for each floral group in each site and year as our response variable (i.e., for each sampling occasion, we summed the densities of all taxa in a given floral group and extracted the maximum value observed for each year and site). We used maximum density instead of total or average density because the first and last flowering of early- and late-blooming taxa, respectively, were missed in some years at some sites. In these models, each replicate represented a yearly metric of floral density for a given floral group in a given site and year. Maximum floral density was natural log-transformed to improve homoscedasticity of residuals. For the RMBL (long-term) data, we combined floral counts across all 21 plots, treating all plots as a single site since they were all located within 1 km of one another. For each floral group, we generated annual metrics of total floral density by summing floral counts across all plant taxa in the group, and across all plots and census days for each year. We then divided total floral counts by the total area surveyed in that year (number of plots surveyed multiplied by 4 m²) to account for differences among years in the number of census days. Total floral density was fourth-root transformed to improve homoscedasticity of residuals.

We ran linear models to test relationships between floral density and water-year drought (drought severity model), as well as water-year precipitation, summer temperature, and their interactive effects (component variable model). For the floral data from the seven sites, we used linear mixed-effects models (LMMs) with site and year (seven and nine levels respectively) included as random-intercept effects. Slope estimates were obtained using the “lmer” function in the “lme4” package (Bates et al., 2015), and significance of fixed factors was evaluated with Satterthwaite-approximated degrees of freedom using the “lmerTest” package (Kuznetsova et al. 2017). We used simple linear models for the RMBL data as each replicate represented floral density for one floral group in a given year. For both datasets, we considered potential variation in responses to climate across the three floral groups by including floral group as an interactive effect with all climate variables (i.e., drought severity * floral group and temperature * precipitation * floral group for the drought severity and component variable models respectively).

Bee reproductive output models

To test the relationships between bee reproductive output, drought severity, precipitation, temperature, and floral abundance, we ran negative binomial generalized linear mixed-effects models (NB-GLMMs) using the “glmer.nb” function in the “lme4” package (Bates et al., 2015). Drought severity, precipitation, and temperature were calculated over a four-month period from May 1 to August 31 (“summer drought severity”, “summer precipitation”, and “summer temperature”), reflecting the months during which female bees were provisioning nests. As with the floral density models, we accounted for potential

interspecific variation in responses to climate by including bee species as an interactive effect with all climate variables. In these models, each replicate represents an individual female of a given species and the total number of brood cells she produced in a given year and site (i.e., lifetime reproductive output). Total brood cell production was recorded as a non-integer variable in the field as we included partially complete brood cells (Figure 2.1d); however, values were rounded to the nearest integer for statistical analysis. Maximum floral density was natural log-transformed to reduce the influence of extreme values. The day of the year on which individual bees were first observed to be nesting (nesting date) was included as a covariate because nesting timing is a known predictor of reproductive success in our study system (Wong and Forrest 2021). Nesting date, precipitation, and temperature were each scaled and centred to mean = 0 and standard deviation = 1. We used the “dispersion_glmmer” in the package “blmeco” to verify that models were not over-dispersed (Korner-Nievergelt et al. 2015).

Table 2.1. Summary of statistical models.

Final versions of models tested. Models are written in the form: response ~ predictor. Model types include linear mixed-effects models (LMMs), linear models (LMs), and negative binomial generalized linear mixed-effects models (NB-GLMMs). Variable transformations and temporal coverage of precipitation, temperature, and drought severity are described in the main text. A priori versions of models contained interactive effects between climate variables and floral group or bee species for models (1–2) and (3–4) respectively. These interactions were removed as they were found to be non-significant; the statistical results reported in the text reflect these reduced models.

Model type	Response	Model Predictors	#
LMM	Maximum floral density (2013-2022)	~ Drought severity + Floral group + (1 Site) + (1 Year)	1a
		~ Precipitation * Temperature + Floral group + (1 Site) + (1 Year)	2a
LM	Total floral density (1976-2022)	~ Drought severity + Floral group	1b
		~ Precipitation * Temperature + Floral group	2b
NB-GLMM	Bee reproductive output (2013-2022)	~ Drought severity + Nesting date + Max. floral density + (1 Site) + (1 Year) + (1 Bee species)	3
		~ Precipitation * Temperature + Nesting date + Max. floral density + (1 Bee species)	4

Structural equation models

We also examined the relationships among climate variables, floral resources, and bee reproductive output at our sites using structural equation models (SEMs), as they facilitate the detection of direct and

indirect relationships and allow for causal inferences to be made from observational data (Shipley 2016). SEMs were constructed and evaluated using the “piecewiseSEM” package in R (Lefcheck 2016).

We constructed two a priori causal networks: the first used drought severity as the predictor for floral density and bee reproductive output; the second used component variables as predictors (Figure 2.4). A priori component models were modified versions of Models 1a and 3 (drought severity) and Models 2a and 4 (component variable) in Table 2.1. In a priori models, we only included interactions that were found to be significant in the linear models described above. Floral group (3 levels) was included as a random effect in component models predicting floral density because including it as a fixed effect (as in the LMMs) complicated results interpretation (standardized estimates cannot be generated for some pathways when models contain categorical fixed effects). The calculation of standardized coefficients has not yet been implemented for NB-GLMMs through the piecewiseSEM package, so we calculated coefficients for all pathways leading to brood cell production using the observation-empirical approach (Grace et al. 2018). We included all pair-wise combinations of correlations between climate variables to account for any covariance between precipitation and temperature, or between climate variables covering different time windows (e.g., summer and water-year drought severity). Response variables and predictors were transformed as in linear models and continuous variables were automatically scaled by piecewiseSEM. Table S2. 9 contains a summary of all component models.

We evaluated model goodness-of-fit using Fisher’s C ($p > 0.05$ indicating adequate fit) and Shipley’s tests of directed separation (d-sep) to identify missing pathways among variables (significant independence claims; Shipley 2016). When d-sep tests indicated that a priori networks were missing biologically plausible significant relationships, we revised component models and reran SEMs (Arif and MacNeil 2023).

2.4 Results

2.4.1 Climate

From 2013 to 2022, our study region sustained two periods characterized by extremely hot and dry conditions: in 2018 and between 2020 and 2021, drought indices neared or surpassed 1.5 for more than half the year, suggesting that conditions were outside the range of normal climatic variation (review in Slette et al., 2019; Figure S2. 1 & Figure S2. 2). Since the start of the long-term flower monitoring in 1976, there had only been three other similarly extreme droughts in terms of magnitude and duration

(Figure S2. 1a; 1977, 1981, and 2012; Prather et al. 2023). Relative to the baseline period of 1976–2012, total annual precipitation fell below the 15th percentile in 2013, 2018, and 2021 (Figure S2. 1b) and mean annual temperatures at the RMBL surpassed the 90th percentile in 2015, 2017, and 2018 (Figure S2. 1c).

2.4.2 Floral density

The effects of drought severity, temperature and precipitation did not vary significantly by floral group; interactions between climate variables and floral group were therefore removed, and we present the reduced models here (final forms of models in Table 2.1). Floral density decreased with increasing drought severity in both datasets, although this relationship was only marginally significant at the seven sites (RMBL: Figure 2.2a; $\beta = -0.06$, SE = 0.01, $t = -4.22$, $p < 0.01$; seven sites: Figure S2. 3a; $\beta = -0.18$, SE = 0.08, $t = -2.24$, $p = 0.06$). At the RMBL, this decrease represented a halving of the number of flowers per m² (per floral group) between the least and most severe drought years. The interactive effect of water-year precipitation and summer temperature was a significant positive predictor of floral density at the RMBL and at our seven study sites (RMBL: $\beta = 0.05$, SE = 0.01, $t = 3.52$, $p < 0.01$; 7 sites: $\beta = 0.16$, SE = 0.07, $t = 2.46$, $p = 0.02$). Visual inspection of interaction plots for both datasets suggested that hot summers had stronger negative effects on floral density when they were also dry (RMBL: Figure 2.2 b–d; Seven sites: Figure S2. 4). We note that water-year precipitation and mean summer temperature at the seven sites were highly correlated, so the slopes characterizing the effects of these variables should be interpreted with caution ($r = -0.75$; Figure S2. 8 & Figure S2. 9). See Table S2. 4 for detailed model results.

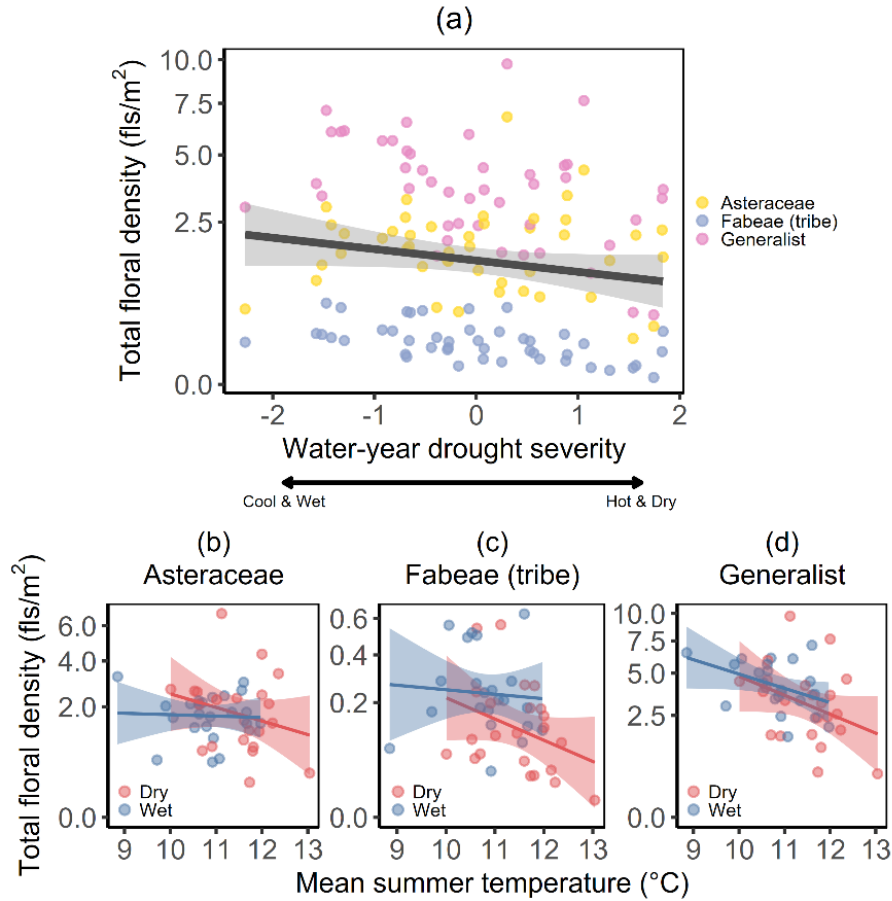


Figure 2.2. Floral density at the RMBL vs. climate variables.

(a) Total floral density at the RMBL (1976–2022) as a function of water-year drought severity (-1×12 -month Standardized Precipitation-Evapotranspiration Index) for all three floral groups. A water-year covers the period between September 1 of the previous year to August 31 of the current year. (b-d): Total floral density at the RMBL as a function of mean summer temperature for each floral group separately. Data are divided into two equal precipitation categories based on total water-year precipitation to visualize the interactive effects of temperature and precipitation. “Dry” and “Wet” correspond to water-year precipitation totals less than and greater than the median water-year precipitation (806 mm), respectively. Red lines have more negative slopes than the blue lines. Each datapoint represents total floral density observed for a given year; $n = 45$ years for each floral group. Bands indicate 95% confidence intervals for the slope of simple univariate linear models. Marginal R^2 values are in Table S2.6. The y-axis was square-root scaled to better visualize all datapoints.

2.4.3 Bee reproductive output

Over nine years, across all sites, we observed the nesting activity of 723 female bees (362 *O. iridis*, 86 *O. coloradensis*, 115 *O. montana*, 115 *O. subaustralis*, 45 *O. tristella*), of which 694 (96%) were successfully paint-marked. Nests constructed by unknown individuals were excluded from analysis;

however, we included 29 unmarked individuals in our analyses because we had ascertained that they were the only unmarked individuals of their species at the given site in that year. On average, females constructed between 6 and 8 brood cells in total (Table S2. 3). Collectively, all individuals in the study produced 5111 brood cells.

Interactions between bee species and climate variables were non-significant in both the drought severity and the component variable models. Models were therefore rerun with bee species (five levels) as a random-intercept effect. Brood cell production decreased with increasing summer drought severity (Figure 2.3a & Figure S2. 6a; $\beta = -0.12$, $SE = 0.06$, $Z = -2.25$, $p = 0.03$), falling from an average of 7.4 to 4.6 cells per female in sites and years characterized by the lowest and highest drought severity respectively. Summer precipitation was not a significant predictor of brood cell production (Figure 2.3b & Figure S2. 6b; $\beta = -0.003$, $SE = 0.06$, $Z = -0.057$, $p = 0.95$); however, hotter summers were associated with significantly lower reproductive output (Figure 2.3c & Figure S2. 6c; $\beta = -0.17$, $SE = 0.08$, $Z = -2.10$, $p = 0.04$). Total brood cell production fell from an average of 10.2 to 4.3 cells per female in the coolest and hottest sites and years, respectively. Maximum floral density was a significant positive predictor of total brood cell production in both the drought severity and component climate models (Figure 2.3d & Figure S2. 6d; drought severity model: $\beta = 0.12$, $SE = 0.03$, $Z = 3.67$, $p < 0.01$, component variable model: $\beta = 0.12$, $SE = 0.03$, $Z = 3.90$, $p < 0.01$). In all models, nesting date was a significant negative predictor of total brood cell production; bees who nested earlier in the season produced more offspring (Figure S2. 7; drought severity model: $\beta = -0.38$, $SE = 0.04$, $Z = -10.56$, $p < 0.01$; component variable: $\beta = -0.38$, $SE = 0.03$, $Z = -10.57$, $p < 0.01$). See Table S2. 5 for detailed model results.

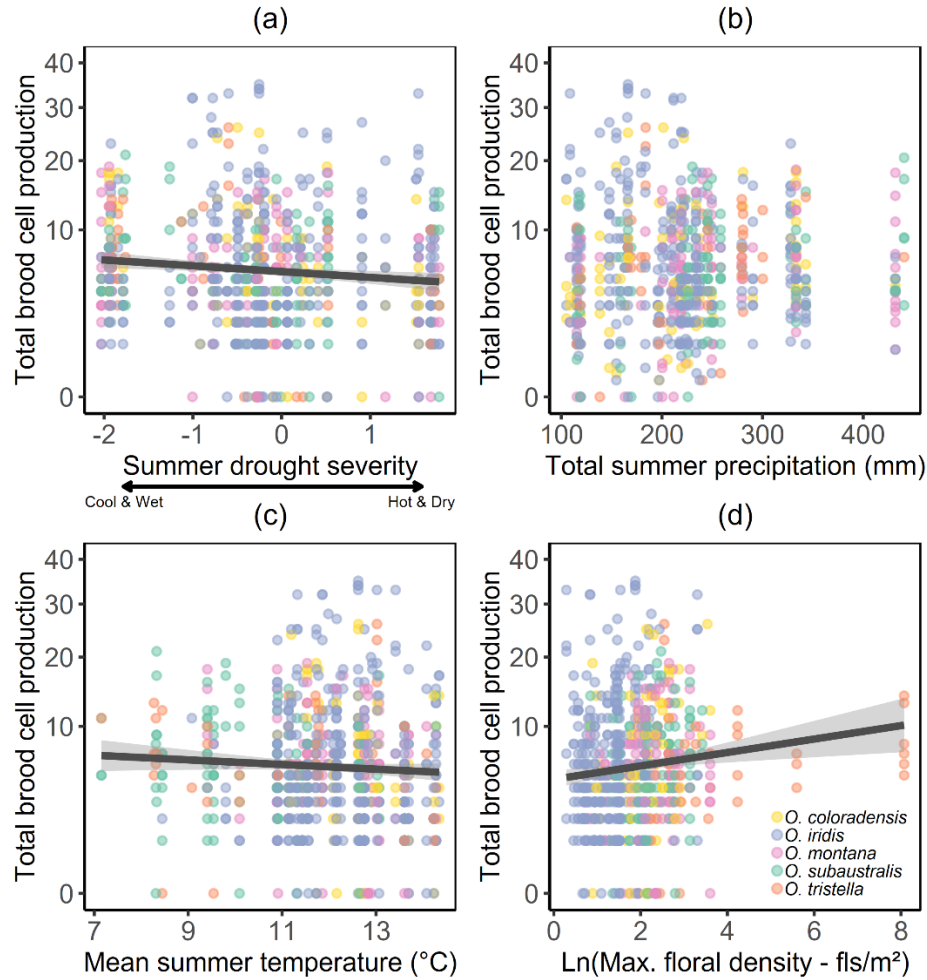


Figure 2.3. Bee reproductive output vs. climate variables and floral density.

Total brood cell production as a function of (a) summer drought severity ($-1 \times$ Standardized Precipitation-Evapotranspiration Index), (b) total summer precipitation, (c) mean summer temperature, and (d) maximum floral density (natural log transformed). Summer = May - August. Each datapoint represents the lifetime reproductive output of one female bee. $n = 723$ individuals in total (*O. coloradensis*: $n = 86$, *O. iridis*: $n = 362$, *O. montana*: $n = 115$, *O. subaustralis*: $n = 115$, *O. tristella*: $n = 45$). An extreme outlier was omitted here for visualization but was retained in all analyses (figures including this datapoint in Figure S2. 5). Solid lines indicate significant ($p < 0.05$) relationships in the multivariate models described in the text. Species-specific trendlines were not included as we did not detect significant interactions between predictors and bee species but figures for each species separately are in Figure S2. 6. The y-axis was square-root scaled to better visualize all datapoints on the same graph. Marginal R^2 values for each predictor are in Table S2. 6.

2.4.4 Structural equation models

The a priori model fit for the drought SEM was inadequate (Fisher's $C = 14.20$, $df = 6$, $p = 0.03$). The path between summer drought severity and maximum floral density was identified as a significant

missing pathway (Fisher's $C = -2.15$, $df = 22.31$, $p = 0.04$; a priori, summer drought severity was only a predictor for bee reproductive output). Model fit was adequate after the addition of this path (Fisher's $C = 7.37$, $df = 4$, $p = 0.12$). No additional missing paths were suggested in the revised model, which suggested both direct and indirect negative effects of drought on bee brood cell production (Figure 2.4a). Increased summer drought severity directly lowered bee brood cell production ($p = 0.03$) but also had a direct negative effect on maximum floral density ($p = 0.04$) which in turn positively affected brood cell production ($p < 0.01$).

Model fit of the a priori component variable SEM was adequate (Fisher's $C = 5.515$, $df = 6$, $p = 0.48$) and revealed significant direct and indirect negative effects of warmer and drier conditions on brood cell production (Figure 2.4b). Increased mean summer temperature was directly associated with lower bee brood cell production ($p = 0.04$). The interactive effects of water-year precipitation and summer temperature were directly associated with maximum floral density ($p < 0.01$), which in turn directly increased bee brood cell production ($p < 0.01$).

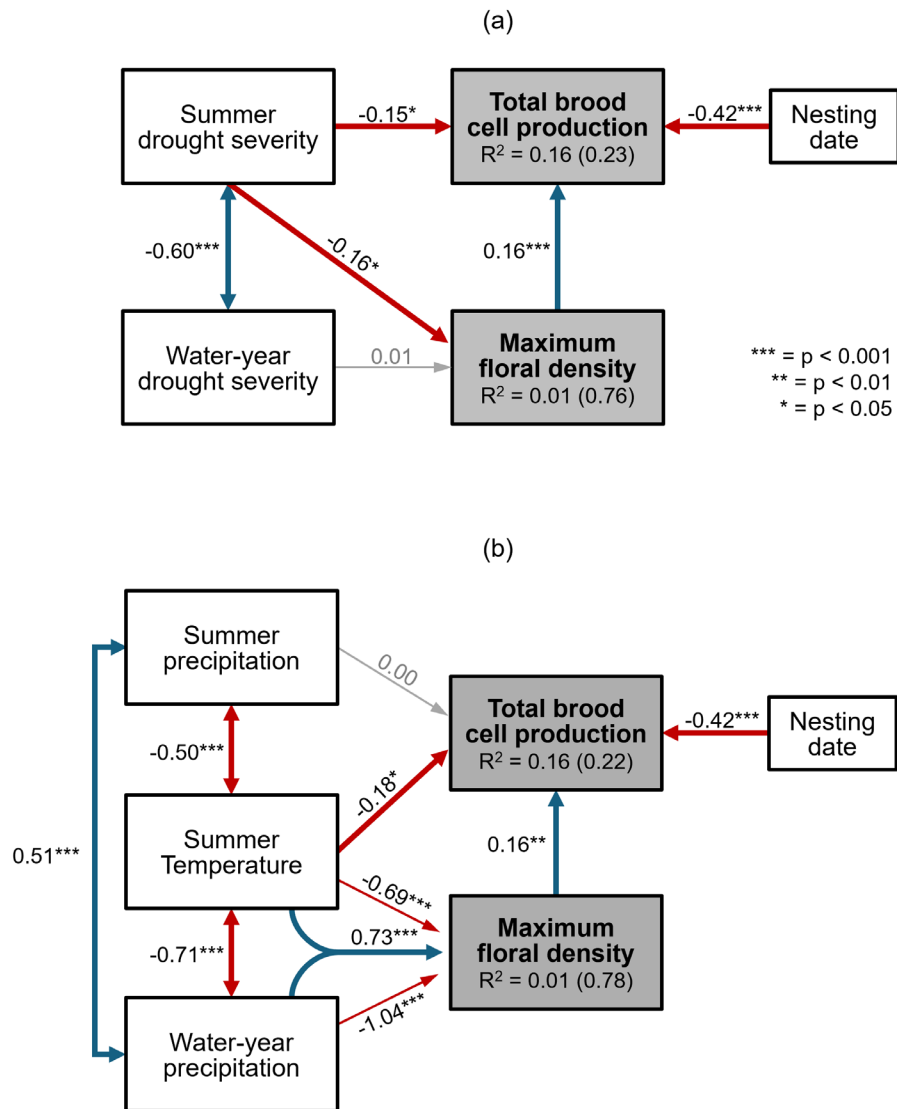


Figure 2.4. Structural equation model.

Structural equation model relating (a) drought severity and (b) climate variables to maximum floral density and total brood cell production of female bees (5 bee species, 7 sites, 9 years; $n = 723$ female bees; sample size by species in Figure 2.3). Single-headed arrows represent unidirectional relationships (“direct effects”). Double-headed arrows represent correlations. Blue and red lines denote significant positive and negative pathways respectively. Grey lines indicate non-significant paths specified in the a priori model. Merged arrow in (b) represents an interaction. Standardized regression coefficients are in standard deviation units. Marginal and conditional (in parentheses) R^2 values are reported for each response variable (grey boxes). Component models for both SEMs are listed in Table S2. 9.

2.5 Discussion

Our observations of over 700 female bees, repeated surveys of floral abundance, and records of precipitation and temperature over nine years, suggest that bee reproductive success in our study system declines with warmer and drier climate conditions and increasing drought severity. We discuss the putative direct and indirect mechanisms that may be at play herein, as well as the potential consequences for populations of bees and other flower-visiting insects in our study area if droughts become increasingly frequent and severe.

2.5.1 Direct effects of climate variables on bee reproduction

Temperature

For many ectotherms, numerous physiological processes including those involved in egg maturation and oviposition are highly temperature-sensitive (Howe 1956, Kingsolver and Huey 2008, Berger et al. 2008, Zhang et al. 2015). In our data, bee brood cell production declined with increasing drought severity and warmer mean summer temperatures, independently of floral density. This pattern could reflect physiological relationships between temperature and reproduction; many insects oviposit only within specific temperature ranges, and egg maturation may be disrupted if temperatures exceed certain thresholds (Engelmann 1970). In laboratory studies with *Osmia* species, higher temperatures have been shown to accelerate oocyte degeneration and arrest oocyte development (Maeta and Kurihara 1971).

The negative relationship we observed between drought conditions and brood cell production could also be driven by the effects of temperature on other aspects of physiology not directly related to egg production. High temperatures can increase oxidative damage and mutation rates in many animals, leading to decreased survival and longevity (Pearl 1928, Burraco et al. 2020, Ritchie and Friesen 2022) and ultimately shortening the time available for reproduction. Indeed, negative effects of high temperatures on longevity, and the resulting loss of time to reproduce, have been previously suggested in our study system (Wong and Forrest 2021) and in another *Osmia* species (Müller et al. 2025). In both studies, the number of days over which females actively nested declined with warmer temperatures, and shorter nesting duration was associated with lower total brood cell production.

Many physiological traits in ectotherms initially respond positively to warmer temperatures but decline rapidly once a species-specific threshold is surpassed (Huey and Stevenson 1979). Although the thermal thresholds of our focal species have not been quantified, laboratory studies with other *Osmia* species have suggested that temperatures exceeding optimal ranges by 3 to 4 °C can generate significant negative

physiological responses including decreased body size, longevity and survival (Kemp and Bosch 2005, Sgolastra et al. 2012, Ostap-Chec et al. 2021). Given that summer temperatures in our study covered a 7 °C range across sites and years, it is plausible that the negative association between drought and brood cell production (independent of floral resources) reflects some direct physiological effects of temperature on nesting females, though we cannot identify the specific mechanisms implicated.

Precipitation

We detected no direct effects of precipitation on bee brood cell production. In general, adult bees are thought to be less sensitive to desiccation than most terrestrial insects, given their nectar diet and ability to generate metabolic water during flight (Nicolson 2009). However, other studies have suggested that bees are prone to desiccation should humidity levels fall below their taxon-specific thresholds, and that desiccation tolerances of bees can predict their abundances (Burdine and McCluney 2019, Kazenel et al. 2024). Separating the effects of precipitation from temperature in observational studies can be challenging, as periods of high temperatures typically co-occur with decreased precipitation. This was the case in our study system, but the correlation between temperature and precipitation was sufficiently modest that we were able to statistically disentangle the effects of both variables (Pearson's r for summer precipitation and temperature = -0.5; Figure S2. 8 & Figure S2. 9). Our results suggest that the direct harmful effects of high temperatures exceeded those of low precipitation.

2.5.2 Indirect effects of climate variables on bee reproduction

Floral density

Floral abundance declined in years characterized by greater drought severity (albeit non-significantly at the seven study sites). This result was unsurprising given that water and heat stress can decrease rates of photosynthesis (Pandey et al. 2015), leaving plants with fewer resources to invest in flower production and/or floral rewards, among various other physiological responses (e.g., reduced vegetative growth, shifts in tissue composition, increased investment in chemical defenses; (Morrison and Stewart 2002, Waser and Price 2016, Descamps et al. 2018). Notably, many plant taxa in our study area are considered relatively drought-tolerant as long-lived perennials with deep taproots; however, the degree to which floral density decreased with increasing drought suggests that drought conditions in our study region reached severity levels beyond the tolerance of even these taxa. We note that there may have been site-specific responses with regards to the effects of hot and dry conditions on floral density. Specifically, floral density at our highest-elevation site actually increased with increasing summer drought severity (data not shown),

suggesting that the negative effects of hot and dry conditions may be less severe at sites that were historically cooler and wetter.

The impacts of drought sustained by plants can have cascading effects on the demographic success of organisms at higher trophic levels—a relationship that has been shown in a range of taxa, e.g., herbivorous insects, frugivorous birds, grazing mammals, seed predators (Fuaborg 1982, McCluney et al. 2012, Kansman et al. 2021). The magnitude of plant-mediated indirect effects may depend in part on the strength of the relationship between plants and their consumers. Females of most bee species are dependent on floral resources to provision offspring and to sustain their own energy demands (review in Roulston and Goodell 2011)—a relationship apparent in our data, which suggested positive relationships between brood cell production and the abundance of the specific floral hosts used by each bee species. While numerous studies have documented positive relationships between floral resource availability and bee abundance and diversity (e.g., Carvell et al. 2004, Hines and Hendrix 2005, Williams et al. 2015), few have directly linked brood cell production in individual bees to local floral resource availability (but see Minckley et al. 1994). Our data builds on the general correlations between bee abundance and floral resources shown in other studies by providing demographic evidence that local floral abundance can increase reproduction, and that brood cell production can be limited by floral resources rather than by physiological limitations on egg production (Minckley et al. 1994). Indeed, we even observed female bees constructing nests consisting only of mud wall partitions, but devoid of pollen provisions and eggs, during periods of low flower abundance, often coincident with lack of rainfall (personal observations). Overall, the positive relationship we observed between brood cell production and floral resources, coupled with our finding that floral resources declined in hot and dry years, suggests that drought had an indirect negative effect on bee fitness via changes in resource availability.

Other indirect pathways

While we explicitly quantified floral density as a mediator of the effects of drought, we acknowledge that other extrinsic variables may have also mediated indirect relationships between drought and bee reproduction. Indeed, any unmeasured variable that covaried with drought and bee reproductive output but not with floral density could have contributed to the “direct” effects of drought severity and temperature in addition to the possible physiological mechanisms described above. For example, bee nests can be attacked by a variety of predators, pathogens, parasitoids and parasites, including brood parasites (Roulston and Goodell 2011)—the prevalence and activity levels of which can be influenced by temperature (Meeus et al. 2018, Palmer-Young et al. 2019). In our study system, one of the most abundant brood parasites is a sapygid

wasp (*Sapyga* sp.). Female sapygids opportunistically enter bee nests while they are in progress and oviposit through the cell partition nearest the nest entrance. Sapygid larvae consume host eggs along with the pollen provision supplied by the nesting female bee. Female bees in our study system have been observed prematurely sealing nests that have been parasitized (i.e., sealing cavities even if they only contain one or two brood cells instead of fully exploiting the length of the cavity; personal observations). Increased parasite activity with warmer temperatures, a pattern previously documented at our sites by Forrest & Chisholm (2017), may have resulted in female bees allocating more time and energy toward nest-sealing and locating new cavities instead of provisioning more brood cells. It is also possible that upon perceiving more parasite activity in their nesting environment, female bees spent less time away from their nests foraging to remain on guard for parasites, although Forrest & Chisholm (2017) suggest that this was not the case at least for *O. iridis*. Notably, sapygids, which attack only two of our five focal species—*O. iridis* and *O. tristella*—are not the only natural enemies attacking *Osmia* spp. in our study area: attacks by the kleptoparasitic bee *Stelis montana* (Megachilidae), chalcidoid wasps, and the predatory beetle *Trichodes ornatus* (Cleridae) have also been observed. Characterizing the role of natural enemies such as brood parasites in driving indirect relationships between climate and bees ultimately requires knowledge of host ranges and the responses of both hosts and parasites to rising temperatures.

The negative relationship we observed between drought and bee reproductive output could also be mediated by pollen and nectar quantity and/or quality (e.g., pollen macronutrients, nectar volume and concentration). Our floral surveys captured changes in floral quantity; however, drought can decrease the quality and quantity of nectar and pollen available to foraging bees (Descamps et al. 2021), an effect that has been linked to negative reproductive outcomes for bees including *Osmia* (Walters et al. 2024). Warmer temperatures can also increase the activity of other flower-visiting insects, potentially causing further reductions in pollen and nectar availability for our focal species. This explanation is plausible given that floral visitors such as bumble bees and flies at our sites were typically far more abundant than our focal taxa (personal observations), and the foraging activity of these taxonomic groups often responds positively to temperature (Corbet et al. 1993, Totland 1994, Goodwin et al. 2021).

2.5.3 Relative importance of “direct” and indirect effects of climate

Ultimately, relationships between climate variables and the reproductive output of organisms reflect combinations of—and interactions between—numerous factors which can be intrinsic or extrinsic to the organisms themselves. In observational studies, the relative contributions of these factors can be difficult to determine, even when they are explicitly quantified. Structural equation modelling allows the relative

strength of direct and indirect pathways between variables in observational studies to be evaluated by comparing the magnitude of standardized coefficients. The overall magnitude of indirect effects can be determined by multiplying the standardized coefficients of the component pathways (Figure 2.4). Our SEMs suggested that the negative effects of drought on bee reproductive output were only partially driven by its effects on floral abundance. The role of other mechanisms that were not quantified in this study—be they physiological (i.e., “direct” sensu stricto) or unquantified indirect effects extrinsic to the bees—had a greater influence in driving the observed negative relationship between drought conditions and bee reproductive output. This result contrasts with findings of similar work in our study area which found that the negative effects of drought conditions on bumble bee abundance were driven mostly by indirect effects mediated by floral resources (Ogilvie et al. 2017). We note, however, that in addition to differences in how floral abundance and bee responses were quantified between the two studies, our focal species exhibit substantially different natural history traits from the bumble bee species studied by Ogilvie et al. (2017), which were larger-bodied, social pollen generalists, with better abilities to regulate their body temperature and that of developing brood (Heinrich and Esch 1994). Understanding the processes underlying climate-fitness relationships ultimately necessitates detailed knowledge of a given study system’s natural history such that important drivers of reproductive success—which may be taxon- or habitat-specific—can be identified and accounted for.

2.5.4 Interspecific variation in responses to climate

We did not detect taxonomic variation in climate responses, i.e., interactions between climate variables and floral group or bee species were not significant; however, we may have lacked sufficient power to detect such interactions. Indeed, the marginally significant interaction between drought severity and floral group in the RMBL data ($p = 0.07$; Table S2. 7) suggested that Fabaeae (tribe) and generalist host floral density responded more negatively to increasing drought compared to Asteraceae floral density. The Asteraceae species in our study area are generally more drought-tolerant than non-aster taxa given their deep taproots (personal observations), possibly reducing the indirect negative effects of drought on brood cell production for bee species that forage from asters (all species except *O. iridis*). Variation in the responses of the five bee species to the effects of drought is also possible given that they exhibit differences in traits apart from pollen specialization. For example, the five species vary in body size, with average intertegular distance ranging from 1.75 mm for *O. tristella* to 2.70 mm in *O. montana* (appendix in McAulay et al. 2021). Body size is an important determinant of thermoregulatory ability in many ectotherms, given the general biophysical relationships between an organism’s surface-area: volume ratio and excess heat dissipation (Porter and Gates 1969). Notably, whether small or large body size is

favoured in high temperature conditions is highly variable across the studies that have examined this relationship in bees. Improved tolerance to high temperatures among larger species has been suggested by some studies, while others have suggested the opposite pattern, or no relationship at all (Gonzalez et al. 2022, 2024, Pardee et al. 2022). The lack of a general relationship between body size and temperature tolerance may be due to the fact that body size is also linked to numerous ecological traits unrelated to thermoregulation, all of which may be implicated in the responses of bees to drought, e.g., nutritional requirements, competitive ability, and foraging distance (Gonzalez et al. 2022, 2024, Pardee et al. 2022). For example, indirect effects of drought mediated by floral resources may have stronger negative impacts on smaller bees as they may be unable to forage greater distances in search of sparsely distributed resources. Whether or not there are patterns between body size and drought response is unclear in our study as *O. coloradensis*, with intermediate body size relative to the other four species, seemed to be the most negatively influenced by drought (Table S2. 8). Incidentally, individuals of this species were also most commonly observed at our lowest elevation (warmer) sites (personal observations; also, compare x-axes of Figure S2. 6c across species). Future studies that aim to understand the processes underlying interspecific variation in the responses of bees to drought would require more information on species-specific physiological tolerances paired with direct observations of their behaviour in the field. Despite differences in pollen specialization and body size, the five focal species in this study are similar in that they are congeneric and are all solitary, cavity-nesting, and semivoltine. More conspicuous variation in climate responses may be expected among bees representing other genera, nesting habits and degrees of sociality.

2.5.5 Future directions

Despite the negative implications of these findings for subalpine bee populations, we note that our predictors—climate, floral resources, and nesting date—explained a modest proportion of the variation in bee reproductive output (marginal $R^2 = 0.16$ in SEMs for brood cell production). The substantial unexplained variation suggests that brood cell production is affected by numerous other variables not quantified here. These variables may be extrinsic or intrinsic to the bees and may or may not be linked to climate. Intrinsic variation in individual reproductive success likely encompasses heritable trait variation, which may influence the capacity of populations to respond via evolutionary adaptation to the increasingly severe droughts predicted for this region. Further work is needed to identify the genetic basis for traits that may confer increased tolerance to drought conditions. Non-genetic adaptive responses to climate change may also be possible; for example, range shifts towards higher elevations and latitudes have already been observed in many taxa, including bumble bees in our study area (Pyke et al. 2016,

Marshall et al. 2020). The capacity for adaptive response to climate change in non-*Bombus* species remains little known but is likely to differ, since the life-history traits and habitat requirements of most bee species are unlike those of bumble bees—which represent less than two percent of all bees. We also note that our study focused on the reproduction component of bee lifecycles, but that drought can influence bee fitness at any point in their lifecycle. How bees at juvenile stages will respond to changes in climate has been little explored in natural populations. Accurate predictions of the consequences of climate change for the persistence of local populations will require an understanding of their responses to climatic variation at all life-stages.

2.6 Conclusion

Despite the preponderance of studies that link changes in climate to widespread global biodiversity loss, the processes driving many of these large-scale patterns remain unclear. Quantifying the in-situ responses of individuals within a population to climate variation is one of the most direct ways to investigate the processes that underlie patterns at large spatial scales. We examined the responses of individually-marked female bees of five focal species to variation in climate and found that warmer and drier years were associated with decreased individual lifetime reproductive output—a relationship partially mediated by declines in floral abundance, but also by additional negative effects of drought. The increasing frequency and severity of droughts predicted for this region (Garfin et al. 2022, Chen et al. 2025) may therefore have important negative consequences for the persistence of these populations if they are not capable of responding adaptively. Long-term individual-level data are critical for delineating the processes that underlie large-scale ecological patterns and for generating predictions about population persistence, yet they are difficult to obtain due to the practical challenges of following individuals over their lifetimes. Such datasets are consequently rare, and among those that exist, invertebrates such as insects are poorly represented, despite the ecological significance of these animals. Our study demonstrates the feasibility of individual-level studies on insects, and our findings highlight the importance of considering how individuals in naturally-occurring populations are responding to environmental change.

2.7 Acknowledgements

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Chapter 3

Beyond the treeline: Are wood-nesting bees and wasps limited by nesting habitat at high elevations?

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The supplementary material associated with this chapter are in Appendix C.

Dr. Jessica Forrest introduced me to the research ideas for this study and together, we refined the overarching research goals and aims. I performed most of the data collection independently with the help of student researchers Rohan Tripathy, Erin Francispillai and Natasha Holy, who contributed to the floral census data. I wrote the code to analyze the data, generated figures, interpreted the data and drafted the manuscript with the guidance of Dr. Forrest.

3.1 Abstract

Although climate suitability is often thought to be the most important determinant of species ranges, non-climate variables such as biotic interactions, dispersal abilities, and habitat quality may play equally important roles as range-limiting factors. For some organisms, the constraints imposed by these non-climate variables may explain their failure to establish in novel habitats that appear suitable with respect to climate. Determining whether or not organisms can respond to rising temperatures via range shifts therefore requires understanding the extent to which non-climate variables limit species ranges. We examined the potential for range shifts in montane populations of wood-nesting bees and wasps in the Colorado Rocky Mountains and assessed the extent to which future range shifts to higher elevations may be limited by the lack of wood substrates beyond local treelines. We tracked wood-nesting bee and wasp occupancy in artificial wooden nesting structures placed at increasing elevations from treeline and quantified the relative abundance of wood- versus ground-nesting bees and wasps at each site. Over the course of the study, wood-nesting bee or wasp nesting activity was observed at least once at all sites, regardless of distance from treeline. The total number of nests constructed at each site decreased with increasing elevation; however, the average number of offspring per nest remained constant for the three most commonly observed taxa. The abundance of wood-nesting bees and wasps declined with increasing elevation more rapidly than that of ground-nesting bees and wasps. These findings suggest that wood-nesting bees and wasps are capable of nesting beyond local treelines, but that the extent to which their ranges can shift upwards in elevation may be limited by the lack of nesting substrate. Our work highlights the importance of considering non-climate variables such as essential habitat requirements in evaluating the capacity of organisms to respond adaptively to climate change.

3.2 Introduction

Among the most well-documented biological responses to climate change are range shifts, whereby species distributions shift to track areas of suitable habitat according to their climate niches (Walther et al. 2002). Shifts in the distributions of many species, primarily towards higher latitudes and elevations, have already been observed in a variety of taxa including plants, birds, mammals and invertebrates (Parmesan and Yohe 2003). Projecting future range shifts has become of recent interest, as this information may serve to identify species that are most vulnerable to climate change and establish regions to target for conservation. Most studies that project future range shifts are based on species distribution models—relationships between species' geographic distributions and current climate conditions that are projected to future climate scenarios (Lawlor et al. 2024). At large spatial scales, this correlative approach has produced relatively accurate predictions, at least with respect to the general direction of observed range shifts.

Nevertheless, there is considerable evidence that for many species, ranges have instead changed at rates or in directions that contradict model predictions (Lawlor et al. 2024). In these cases, non-climate variables, such as specific habitat requirements and species interactions, may be constraining the ability of species to shift their distributions to climatically-suitable habitats; yet these variables are rarely integrated into distribution models, which tend to assume that climate is the primary range-limiting factor (but see Gogol-Prokurat 2011, Pollock et al. 2014). Discrepancies between model predictions and realized range shifts may also arise due to mismatches between the spatial resolution of the climate data used in models and the scale at which organisms experience their environment. These spatial scale mismatches may be especially acute for small-bodied species, as their occurrences are likely influenced by conditions at much smaller scales than what is typically represented by gridded (spatially-interpolated) climate data (Tredennick et al. 2021). Evaluating the capacity for range shifts in such species may require an understanding of the range-limiting role of non-climate variables and the characterization of local environmental predictors that reflect what organisms directly experience.

In-situ field studies can help to elucidate the role of non-climate variables that may constrain shifts in species distributions. For example, transplant experiments, whereby populations are established beyond their current known range boundaries, are commonly used to assess the viability of beyond-range populations (Lee-Yaw et al. 2016). However, while transplant studies have been effective for predicting range shifts in plants, similar studies with animals are rare. Transporting non-sessile organisms to new locations can be logistically challenging, and following individuals to assess their viability post-transplant may be impossible if they are highly mobile. Such studies also come with the risks of accidental species

introductions and altered gene flow. An alternative approach to determining factors that limit species ranges may be to examine the extent to which a species' habitat requirements are limiting to population growth or establishment at sites near or just beyond their known range margins. Whether or not the establishment of a population beyond its range margins is limited by habitat requirements can then be inferred.

We applied this latter approach in examining the potential for range shifts in high-elevation populations of wild bees and wasps. Bees and wasps play indispensable roles in many ecosystems as pollinators, predators, and parasitoids (Neff and Simpson 1993, Brock et al. 2021). Climate change-driven range shifts in these insects are of particular interest as many aspects of their life-histories, such as their development, survival, longevity and fecundity, are directly influenced by temperature (Bosch and Kemp 2004, Gurel and Gosterit 2008), yet their ranges may also be constrained by the availability of floral host-plants (bees), prey (wasps), and nesting substrates. The quantity and quality of these habitat variables can themselves be affected by changes in climate; yet shifts in these variables across space and time may not match those of their consumers (Bartomeus et al. 2011).

Climate change-induced range shifts have been documented in some bees (e.g. Kuhlmann et al. 2012, Kerr et al. 2015, Pyke et al. 2016); however, most of these studies focus on the large, eusocial bumble bees (*Bombus* spp.). Bumble bees are important pollinators that are well represented in natural history repositories, but they make up <2% of all bee species and exhibit substantially different life-histories, thermal tolerances, and dispersal capacities from most species. Less is known about range shifts in non-*Bombus* bees and even less in non-social wasps (but see Maihoff et al. 2023). Moreover, most studies that examine range shifts in bees have focused on relationships between bees and climate at large spatial scales, even though the demographic success of these insects is influenced by local-scale variables that may not be well represented by macroscale climate variables. For example, females bees and wasps of most species require flowers and arthropod prey respectively to provision their young; the reproductive output of many species is often limited by the availability of these resources within a few hundred metres of their nests (Roulston and Goodell 2011, Fabian et al. 2014). Considering the range-limiting roles of local habitat variables may therefore be necessary in evaluating the capacity of bees and wasps to undergo range shifts in response to changes in climate.

Many species of solitary bees and wasps construct their nests in existing cavities in aboveground structures (Danforth et al. 2019; O'Neill 2001), including those left in dead wood by other arthropods, such as beetles (hereafter, “wood-nesting bees and wasps”; Krombein 1967). Previous studies have

suggested that the abundance of wood-nesting bees and wasps is predicted by the local availability of wood cavities (Potts et al. 2005, Westerfelt et al. 2015, Hyjazie and Forrest 2024), yet the extent to which this variable could be limiting adaptive responses to climate change among wood-nesting insects is unknown. (Note that use of the term “adaptive” here and throughout this chapter does not necessarily imply an evolutionary process; rather, it describes a behavioural or demographic response that increases the fitness of individuals in a population.) Mountain ecosystems have been experiencing more rapid rates of warming than lower-elevation habitats (Pepin et al. 2015), and many montane organisms have already responded by shifting their distributions upwards in elevation to cooler habitats (e.g., Lenoir et al. 2008, Pyke et al. 2016). However, the scarcity of woody material above high-elevation treelines may limit the extent to which populations of wood-nesting bees and wasps can shift their distributions upslope (e.g., compared to taxa that nest below-ground). Such a mismatch is plausible, since the rate at which flying insects can disperse and potentially expand their ranges likely outpaces the rate at which treelines will shift.

Our study explores the extent to which local availability of nesting substrate may limit future upslope range shifts in high-elevation populations of wood-nesting bees and wasps in the Colorado Rocky Mountains. In recent years, much of southwestern North America, including Colorado, has experienced significantly warmer and drier conditions, with parts of the region having experienced temperature increases far greater than most other regions in the continent (Gonzalez et al. 2018). Previous work in our study area has shown that high temperatures can have negative fitness consequences for wood-nesting bees (Wong et al. 2025) and that the current upper-elevational distributions of certain species already lie close to local treelines (personal observations & see “Study Organisms” below). Given the increasingly warm temperatures forecasted for our study region, these observations suggest that range shifts to higher elevations could be an adaptive response for these populations if they are to remain within thermally-suitable environments. The extent to which future range shifts in high-elevation populations of wood-nesting bees and wasps are constrained by their nesting requirements remains unclear.

We assessed the capacity of wood-nesting bees and wasps to nest successfully above treeline, provided nesting habitat is available, by placing wood nesting structures (“trap-nests”) at increasing vertical distances from local treelines where nesting cavities in wood would have otherwise been scarce or absent. Evidence of nesting activity at these sites would suggest that the lack of nesting substrate at high elevations may constrain upward range shifts in wood-nesting bees and wasps: Any individuals found nesting in trap-nests would have had to successfully disperse to the established site (presumably from treeline), access sufficient food resources to provision their nest and sustain themselves, and tolerate the

abiotic conditions at high elevation (e.g., strong winds, high temperature variance, hypoxic conditions) and reproduce. Observing nesting activity at these beyond-treeline sites would therefore make it unlikely that dispersal, food resources, or abiotic conditions are primary range-limiting factors. We also conducted insect surveys at each site to independently characterize the abundances of wood- and ground-nesting bees and wasps. Here, we viewed ground-nesting bees and wasps as “pseudo-controls” given that their distributions are unlikely to be directly related to the availability of wood nesting substrates.

3.2.1 Predictions

If future upward range shifts in wood-nesting bees and wasps are strongly limited by the lack of nesting cavities at high elevations, but not by availability of food resources or the abiotic environment, we expect: **(1)** the total number of occupied cavities in trap-nests to decrease with increasing elevation as occupants would have to disperse further from source populations (presumably at or below treeline) to access sites. However, if beyond-treeline sites across elevations are similar in quality *except* with respect to distance from naturally-occurring nesting habitat, we expect **(2)** no relationship between elevation and the number of offspring found in nests (i.e., brood cell production). Finally, we expect **(3)** abundances of wood-nesting bees and wasps to decrease more rapidly than abundances of ground-nesting bees and wasps with increasing elevation due to stronger nesting substrate limitation at high elevations for the former.

3.3 Methods

3.3.1 Study sites

Field work was conducted from late June to early August 2021–2023 near the Rocky Mountain Biological Laboratory in Gothic, Colorado (38.9592°N 106.9897°W; 2900 m; Figure S3. 1a). We established 19 high-elevation sites spanning an elevational gradient of 274 m (3443–3717 m) across the slopes of three mountains, with 5–8 sites per mountain: Avery Peak, Mount Baldy, and Gothic Mountain (Figure S3. 1a). Mountains were located at least 3 km apart. Sites on the same mountain were separated by a minimum distance of 60 m (Figure S3. 1b). We note that the definition of “treeline” varies in the literature (Harsch and Bader 2011). For the purposes of this study, we ensured that all sites were at least 200 m beyond the upper limits of continuous forest areas perceptible from the ground. The elevations at which these limits occurred varied between the three slopes. Many solitary bee species forage within 100 m of their nests (Zurbuchen et al. 2010, Kendall et al. 2022); however, their maximum flight distances (i.e., dispersal distances) are generally greater, often exceeding 1 km (reviewed in Murray et al. 2009). Our sites therefore represent habitats an individual from a below-treeline population would be unlikely to encounter on a foraging bout, but that are likely still within their dispersal range. Flight and foraging distances of solitary wasps remain poorly documented; however, given the strong correlations documented between

body size and maximum flight distances in bees (Kendall et al. 2022) and the relatively similar morphologies between the two insect groups, wasp flight capabilities are likely comparable to those of bees.

Each site contained three trap-nests—artificial wooden structures consisting of blocks of untreated lumber each with 10–16 holes of three different diameters drilled into them, for a total of 30 to 42 cavities per site (Figure S3. 1c & d). Holes were lined with paper straws, within which bees and wasps could construct nests. Straws allowed for nests to be temporarily extracted and inspected without disturbing the nest occupants (Figure S3. 1e). All three trap-nests were attached to a wooden stake driven into the ground no more than 0.75 m above the soil surface. As much as possible, all trap-nests for a given mountain were oriented with the nest entrances facing south or southeast; however, consistent orientation across all sites was not always possible given the surface geometry of accessible slopes (i.e., aspect). Because terrain features such as aspect can have a strong influence on local temperature, which could in turn affect our response variables, we derived aspect from digital elevation model data for each site (United States Geological Survey) and verified that its inclusion in statistical models did not change our statistical results.

3.3.2 Study organisms

Past work in our study area has documented the presence of over thirty wood-nesting bee species, primarily in the family Megachilidae (Pardee et al. 2022). Many of these species in addition to several wood-nesting wasp species (Vespidae and Pemphredonidae) have been found occupying trap-nests established for other studies at nearby sites below treeline (Forrest and Thomson 2011). Nests of these trap-nest occupants generally consist of a linear series of brood cells, each containing a food provision (pollen and nectar for bees, arthropod prey for wasps) and a single egg. Cells are typically separated by mud, masticated leaf, pebble or resin partitions constructed by nesting females. Based on our previous observations of trap-nest activity at lower elevations, some females build multiple nests in succession (i.e., use more than one cavity); however, the majority (two thirds of the individuals observed) use only one (Wong et al. 2025). Whether or not these species occurred above 3400 m in this region (elevation of the highest site in previous studies) was unknown at the time of our study. Over eighty ground-nesting bee species have also been documented in our study area with representatives from multiple families (Pardee et al. 2022). Some of these species had previously been observed in our study area at elevations as high as 3800 m (Pyke et al. 2016); however, records from the Global Biodiversity Information Facility

(GBIF) suggest that these were primarily bumble bees and that any observations of wasps beyond 3400 are very rare (unpublished analysis of GBIF specimen records).

3.3.3 Data collection

Trap-nest occupancy

In each year of the study, each site at two of the three mountains (Avery and Baldy; Table S3. 1) was visited between three and five times (with the exception of three sites at Mt. Baldy which were only visited twice in 2021). Trap-nests at Gothic Mountain were visited only once at the beginning and end of each season due to the difficulty of accessing these sites. During each site visit, paper straw liners were briefly extracted from trap-nests and inspected for occupancy. We recorded the date on which nests were first observed and the taxonomic identity of occupants (typically species, but sometimes subgenus or genus). Taxonomic identifications were inferred based on a combination of the occupant's morphological features, nest construction (e.g., wall material, type of provisions, brood cell size), and our knowledge of the most common cavity-nesting bee and wasp taxa in the study area (Forrest and Thomson 2011). Whenever possible, occupants were also temporarily caught and marked with small dots of non-toxic paint on their mesosomas (Figure S3. 1f). These marks allowed trap-nest occupants to be distinguished from other wood-nesting Hymenoptera observed during insect surveys (described below). A unique colour was chosen for every site so that movement of individuals between sites on the same slope could be identified (although this never occurred). The total number of brood cells per nest was recorded for species that constructed visually-distinct brood cells (i.e., nests where each individual brood cell could be seen by holding the paper straw containing the nest up to the light; Figure S3. 1e). These taxa included *Hoplitis albifrons*, *Hoplitis fulgida*, *Hylaeus* spp., *Osmia montana*, *O. subaustralis* and *O. tristella*. In 2022 and 2023, completed (sealed) nests from trap-nests at Avery peak and Mt. Baldy were removed and stored in a weather-proof box at the site. Cavities were then replaced with empty straws to make space for new nests to be built. Sealed nests at Gothic Mountain were not replaced with new straws as trap-nests were sparsely occupied in every year and there were always many available cavities.

Insect surveys

Insect surveys were conducted each time sites were checked for trap-nest occupancy (11–14 surveys per site over the three years). During surveys, a single observer (LHW) noted all sightings of bees or wasps for 30 minutes while walking slowly within a 30-metre radius of the site centre where the trap-nests were located. Sites were divided into four quadrants, with equal amounts of observation time spent in each. Surveys generally occurred during periods of warm, calm and sunny weather. Air temperature and

average windspeed were recorded at the beginning, the fifteen-minute mark, and immediately after each survey using an unshaded Kestrel® 2000 Pocket Weather Meter held 1 m in front of the trap-nests. Bees and wasps were identified in the field to genus. Representative photos for 229 observed insects (10.5% of all observations) were uploaded to iNaturalist (<https://www.inaturalist.org/projects/2021-2023-elk-mountains-insect-surveys-3400-m>) and the identifications of 57% (176 photos) were confirmed by taxonomic experts including John Ascher, Jessica Mullins and Susanna Heideman (full list of names in Table S3. 4). Observations of insects for which taxonomic identifications were unclear and which we were unable to photograph were excluded; this included several tiny, likely parasitic, wasps. In some cases, genus-level identifications were not possible from photos; these insects were therefore identified to family only. In general, this level of taxonomic resolution was sufficient for the purposes of this study as we were interested only in whether observed individuals were wood-nesting or ground-nesting; for the most part, classifications of nesting habits are broadly conserved within families and genera. For example, all species in the bee genus *Andrena* are ground-nesting (Michener 2007). Observations of insects with potentially ambiguous nesting habits were flagged (Table S3. 3), and we examined the effects of their inclusion on our statistical results. Kleptoparasitic bees were assigned the nesting habits of their hosts. A list of all taxa observed, and their nesting habits, are in Table S3. 3. We excluded observations of parasitic wasps in the superfamily Ichneumonoidea (Ichneumonidae and Braconidae) and the family Chrysididae as many species in these groups as well as their hosts (which include ground- and wood-dwelling arthropods) remain undescribed.

Flower surveys

Flower surveys were conducted after every insect survey. In addition to being a predictor of brood cell production in bees (Roulston and Goodell 2011, Wong et al. 2025), floral resource availability is a known predictor of bee and wasp abundance since adults of most species consume floral nectar (Hyjazie and Sargent 2022, Neumann et al. 2024). All open flowers, excluding graminoids, were identified and counted within four 30-m transects radiating out from the centre of each site in the four cardinal directions (Figure S3. 1c). Although 30 m likely underestimates floral resources available to bees nesting in the trap-nests, the primary goal of floral surveys was to characterize the floral landscape at the site for all bees and wasps, regardless of whether or not they were trap-nest occupants. Transects were typically 100 cm wide but were occasionally adjusted to 10 cm or 50 cm depending on the density of the species being counted (i.e., narrower for more abundant species; transect widths were accounted for in calculations of floral density). The floral units counted varied by species (Table S3. 2). *Vaccinium myrtillus*, was hyperabundant (up to 480 flowers/m² on some survey occasions) in each year of the study but was visited

by few flower-visiting insects other than bumble bees. Because periods of hyperabundant *V. myrtillus* often coincided with periods of otherwise low floral abundance, we excluded this species from counts to avoid overestimating floral resources available to most bees and wasps.

3.3.4 Data analysis

General approach

All analyses were conducted in R (ver. 4.4.1; R Core Team 2024). We used negative binomial regression models to evaluate the relationships between our predictor and response variables. For all models we checked for multicollinearity among continuous predictors visually by examining scatterplots of bivariate relationships, and by calculating variance inflation factors (VIFs) using the “car” package (Fox et al. 2001). VIFs did not exceed 2.52, indicating that multicollinearity was not severe. Including site aspect as an additional predictor did not change our results and was therefore not included in our final models. The “DHARMa” package (Hartig 2022) was used to generate diagnostic plots for evaluating model fit and to check for overdispersion. In all models, all continuous predictors were scaled and centred to mean = 0 and standard deviation = 1. Marginal means were estimated using ‘emmeans’ (Lenth and Piaskowski 2025). Models are described in greater detail below.

Trap-nest occupancy data

To examine changes in trap-nest occupancy with increasing elevation (distance from treeline), we ran a negative binomial model using the `glm.nb` function in the “MASS” package (Venables and Ripley 2002) with elevation as a predictor for the total number of nests observed at a given site in a given year. Year and mountain (both with 3 levels) were included as categorical fixed effects and the total number of available cavities at each site was included as a covariate. To test for the effects of floral resource abundance, we ran a second model identical to the first, but with maximum floral density as an additional predictor. Data from Gothic Mountain were excluded from this model since floral density was not quantified at these sites. Maximum floral density was obtained by calculating the total density for every plant taxon recorded in each survey, summing across species to obtain the total density for each survey, and selecting the highest total density recorded across all surveys for a given year and site. Maximum floral density was natural log-transformed to reduce the influence of some extreme values. We also examined the relationship between elevation and the number of brood cells found in each nest. We ran negative binomial generalized linear mixed-effects models (NB-GLMM) using the “`glmer.nb`” function in the “lme4” package (Bates et al. 2015) with elevation and occupant taxon as predictors for the total number of brood cells within a nest in a given site and year. Occupant taxon was included as an

interactive effect with elevation to account for potential interspecific variation in the responses to elevation. *Osmia montana* and *O. subaustralis* (subgenus *Cephalosmia*) were treated as a single taxonomic group as both are specialists on Asteraceae pollen (Spear et al. 2016) and construct morphologically-indistinguishable nests (but see notes in Appendix F). Similarly, we combined *Hoplitis albifrons* and *H. fulgida* into one group given their ecological similarities (pollen generalists, nest construction) and phylogenetic relatedness. *Hylaeus* nests were not included in this model even though their brood cell production was quantified as they made up <1% of observed nests. The three taxonomic groups included in this model were therefore *Cephalosmia* spp., *Hoplitis* spp., and *Osmia tristella*. As with the nest occupancy data, we tested for the effects of floral resources in a separate model that contained total floral density in addition to elevation and occupant taxon with data from Gothic Mountain excluded. Total floral density was that observed on the day on which the nest was first observed and was natural log-transformed. Floral density predictors for *Cephalosmia* brood cell production only included counts of plants in the family Asteraceae. In both models (with and without floral density), year and mountain were included as categorical fixed effects, and site was included as a random intercept effect.

Insect survey data

For each site and each nesting guild (wood- or ground-nesting), we summed the total numbers of insects observed during each survey occasion. Weather variables were averaged across all three measurements taken before, during, and after survey periods. To examine changes in wood- and ground-nesting insect abundance with increasing elevation we ran an NB-GLMM with elevation, nesting habit, and their interaction as predictors for the total number of bees and wasps observed during each survey. The mountain (2 levels), year (3 levels), total floral density for the survey date (natural log-transformed), mean temperature, and mean windspeed were all included as covariates. The date (day of year) on which the survey took place, and the survey start time were also included as continuous predictors to account for seasonal variation in insect abundances and known diurnal patterns of insect activity respectively. Day of year was treated as a linear predictor because all surveys were conducted within a sufficiently short time window (late-June to early-August) that seasonal declines in insect counts were not observed after the initial increase early in the season. Time was included as a second order polynomial because insect counts tended to peak between late-morning and early-afternoon and subsequently decline. Site was included as a random intercept effect. We reran this model with observations of insects with ambiguous nesting habits excluded (see “Insect surveys”, above). We also reran this model with bumble bees excluded because their life-history differs substantially from most other bees and wasps at our sites, and because their large size and conspicuousness may have led to them being overrepresented in the data.

3.4 Results

3.4.1 Trap-nest occupancy

All sites at all three mountains had at least one trap-nest occupant over the three years of the study. Across all sites and years, we observed a total of 740 nests, 671 (91%) of which were constructed by bees, 56 by wasps, and 13 by occupants that were likely bees but that could not be determined with certainty. Bee occupants included *Osmia subaustralis* Cockerell, *O. montana* Cresson, *O. tristella* Cockerell, *Hoplitis fulgida* Cresson, *H. albifrons* Cresson, *Megachile relativa* (all Megachilidae), and *Hylaeus* spp. (Colletidae). Wasp occupants included vespids in the subfamily Eumeninae (*Ancistrocerus* and possibly *Symmorphus* spp.) and pemphredonids in the genus *Passaloecus* (Figure S3. 2). The total number of occupied cavities decreased significantly with increasing elevation (Figure 3.1; $\beta = -0.53$, SE = 0.11, $p < 0.01$), with a 6-fold decrease in the model-predicted number of nests at the highest-elevation site relative to the lowest-elevation. The relationship between nest occupancy and elevation remained the same when maximum floral density was included in the model and data from Gothic Mountain were excluded ($\beta = -0.51$, SE = 0.11, $p < 0.01$). Maximum floral density was not a significant predictor of the number of occupied cavities (Figure S3. 3; $\beta = 0.18$, SE = 0.12, $p = 0.15$).

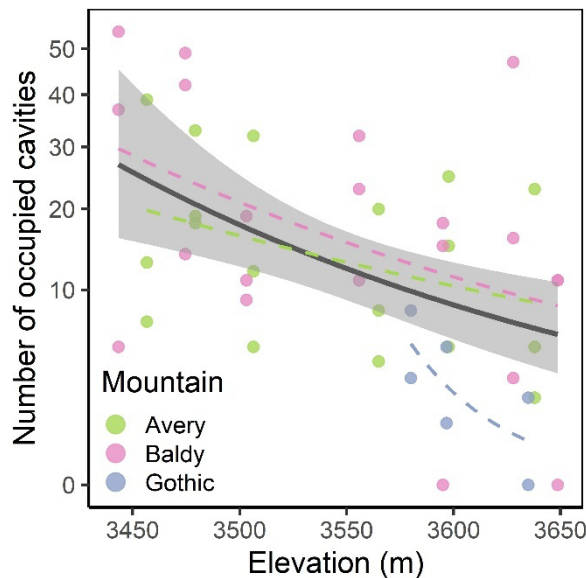


Figure 3.1. Trap-nest occupancy vs. elevation.

Number of occupied cavities as a function of elevation at 19 sites from 2021 to 2023. Each datapoint represents the total number of occupied cavities at a given site on one of three mountains in a given year of the study (see Table S3. 1 for mountain details). $n = 18, 24$, and 10 unique year-mountain-site combinations for Avery, Baldy, and Gothic respectively. Solid lines indicate significant ($p < 0.01$) relationships in the multivariate models described in the text for all three mountains combined. The grey band represents a 95% confidence interval for the slope of a simple univariate linear model. Dashed lines for each mountain are for visualization only (the elevation * mountain interaction was not significant). Datapoints were jittered, and y-axis was square-root scaled for visualization.

3.4.2 Brood cell production

We quantified brood cell production in 336 *Cephalosmia* nests, 118 *Hoplitis* nests, and 134 *O. tristella* nests. Cumulatively, these nests contained 3422 brood cells across all sites and years. The effect of elevation on the number of brood cells per nest did not vary significantly between the three taxonomic groups included in the analyses, so we reran the model with elevation and occupant taxon as independent fixed effects. Elevation was not a significant predictor of the number of brood cells per nest (Figure 3.2. $\beta = -0.05$, $SE = 0.03$, $p = 0.12$). This result was unchanged by the addition of floral density to the model ($\beta = -0.05$, $SE = 0.03$, $p = 0.13$). Floral density was a significant, albeit surprisingly negative, predictor of brood cells per nest (Figure S3. 4; $\beta = -0.12$, $SE = 0.04$, $p < 0.01$).

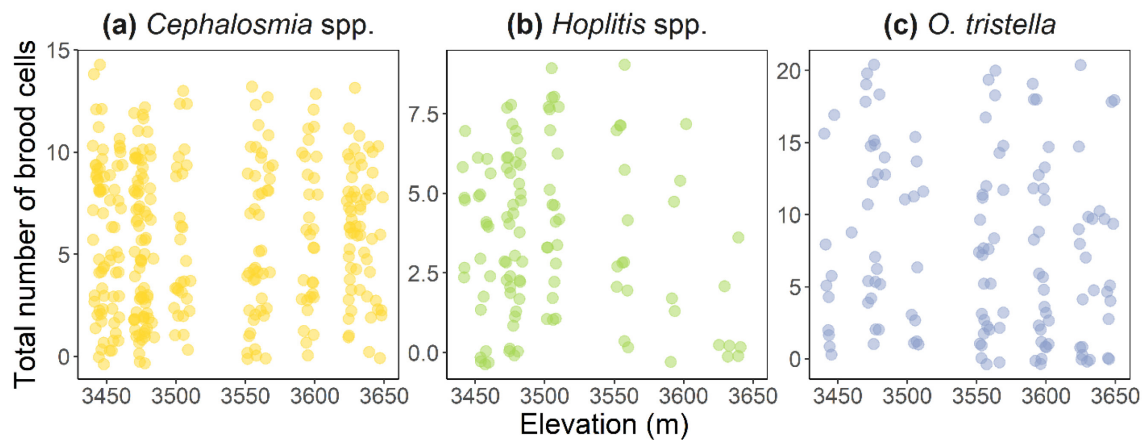


Figure 3.2. Brood cells per nest vs. elevation.

Number of brood cells per nest for (a) *Cephalosmia* spp. (*Osmia subaustralis* and *O. montana*), (b) *Hoplitis* spp. (*H. albifrons* and *H. fulgida*), and (c) *Osmia tristella* as a function of elevation at 19 sites from 2021 to 2023. Each datapoint represents one nest (i.e., the total number of brood cells in one nest constructed by an individual of one of the three taxonomic groups at a given site on one of three mountains in a given year of the study). Sample sizes for (a), (b), and (c) are as follows: $n = 336$, 118, and 134 nests respectively. Datapoints were jittered for visualization.

3.4.3 Insect surveys

A total of 2950 insects were observed during surveys across all sites and years of the study (84.5 observation hours). Bees represented 87.4% of all observations. The most common taxa observed were the ground-nesting genera *Bombus* (36%), *Lasioglossum* (20%), and *Panurginus* (16%). Across all sites and years, the number of ground-nesting bees and wasps observed was nearly 16 times greater than the number of wood-nesting insects observed (2775 ground-nesting, 175 wood-nesting). Wood-nesting bee and wasp abundance decreased with increasing elevation significantly more rapidly than ground-nesting

bee and wasp abundance (elevation * nesting habit interaction: Figure 3.3; $\chi^2 = 4.77$, $df = 1$, $p = 0.03$). This result remained unchanged when bumble bees (*Bombus* spp.) were excluded from the model ($\chi^2 = 4.57$, $df = 1$, $p = 0.03$) but was no longer significant once observations of insects with ambiguous nesting habits were removed ($\chi^2 = 3.25$, $df = 1$, $p = 0.07$). Floral density was a significant positive predictor of overall insect abundance (Figure S3. 5a; $\beta = 0.12$, $SE = 0.05$, $p < 0.01$); however, this was no longer the case when bumble bees were excluded (Figure S3. 5b; $\beta = 0.04$, $SE = 0.06$, $p = 0.45$).

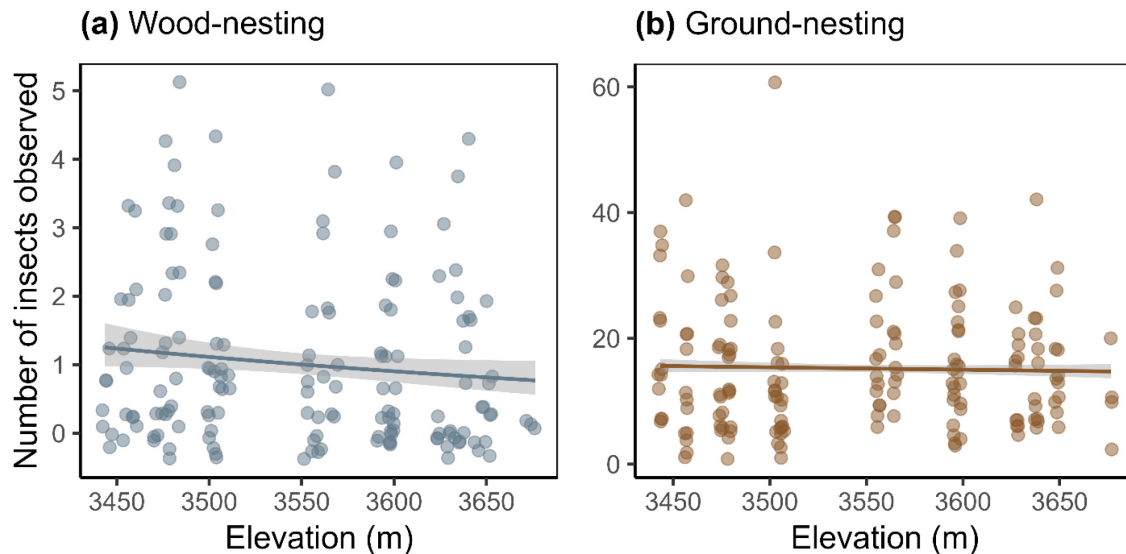


Figure 3.3. Cavity-nesting and ground-nesting insect abundance vs. elevation.

Numbers of (a) wood-nesting and (b) ground-nesting bees and wasps observed as a function of elevation. Each datapoint represents the total number of bees and wasps observed during a 30-minute survey period. $n = 169$ surveys at 14 sites (2 mountains) and 3 years. Insect surveys were not conducted at the five sites on Gothic Mountain; see Table S3. 1. Datapoints were jittered for visualization. Note the different y-axis scales between the two panels.

3.5 Discussion

The capacity of organisms to respond to changing climate conditions by shifting their distributions is jointly dependent on their ability to disperse to sites beyond their current range margins and to reproduce successfully once there. Our findings suggest that the wood-nesting bees and wasps in our study system were able to meet both criteria, as females were observed provisioning nests in artificial structures placed beyond local treelines—their putative range margins. Nevertheless, despite the apparent suitability of these sites with respect to flight distances from treeline and environmental conditions for nest provisioning, had the sites not been artificially supplemented with nesting substrate, wood-nesting bees

and wasps might have been unable to establish given the sparsity of naturally-occurring wood at these elevations. We therefore suggest that the lack of wood substrates beyond the treeline may play an important role in limiting the upper-elevational distributions of high-elevation populations of wood-nesting bees and wasps, potentially constraining their ability to respond adaptively to climate change via upslope range shifts.

3.5.1 Limiting factors for alpine insects

Dispersal limitation is often thought to explain the failure of species to occupy climatically suitable habitat and undergo range shifts (Schloss et al. 2012, Laube et al. 2013); however, our nest occupancy data suggested that dispersal is unlikely to be the primary range-limiting constraint in our study system: each site, regardless of elevation, was occupied at least once by a wood-nesting occupant over the course of the study. We note that some degree of dispersal limitation may still be at play given that the total number of occupied nests we observed in trap-nests decreased with increasing elevation—a result that likely reflects the increasing distances required of occupants to disperse from their natal sites, which are presumably at or below treeline (Prediction 1). Nevertheless, the successful colonization of each site suggests that all sites were within the maximum flight ranges of at least some wood-nesting bee and wasp taxa.

Even if they were not limited by dispersal, organisms could still fail to undergo range shifts if the local environmental conditions at beyond-range sites impede their ability to survive and reproduce. For example, successful beyond-range establishment may be limited by a lack of resources (e.g., food, nesting material), presence or absence of biotic interactions, or by abiotic (Joyner-Matos et al. 2007, Louthan et al. 2015). In our study system, wood-nesting bees and wasps could find it impossible to provision nests at high elevations if they were unable to access sufficient food resources or if weather conditions were too cold and windy for efficient flight. Our observations of wood-nesting bee and wasp nesting activity (i.e., constructing and provisioning nests, laying eggs) suggest that beyond-treeline reproduction is not precluded by unfavourable environmental conditions. Indeed, our finding that per-nest brood cell production did not change with increasing elevation (Prediction 2) suggests that our beyond-treeline sites were likely similar in quality except with respect to elevation (distance to treeline). Notably, we are not suggesting that there were no environmental constraints on brood cell production beyond local treelines in our study system. If anything, the significant negative relationship between brood cell production and increasing floral density we observed likely reflects the negative effects of some other unmeasured environmental variable on brood cell production that happens to covary with floral density (e.g., abundances of parasites or floral resource competitors). That said, our data suggest that this

environmental constraint, irrespective of its identity, was no more limiting at higher elevations than it was at sites closer to treeline. Our findings therefore suggest that the upper-elevational range limits of the wood-nesting bees and wasps in our study are unlikely to be driven by environmental constraints on reproduction.

One limitation of our study is that it is unclear whether wood-nesting bees and wasps occurred beyond the treeline in our study area prior to the establishment of our sites (and trap-nests). It is possible that the krummholz growth and isolated trees present beyond the treeline allowed small local populations of wood-nesting bees and wasps to persist at these sites independently of our trap-nests. Plasticity in nesting behaviour of our focal taxa—specifically, willingness to exploit pre-existing cavities in other substrates such as hollow plant stems and cracks in stone (Cane et al. 2007) could have also enabled populations to exist beyond local treelines. The decrease we observed in trap-nest occupancy with increasing elevation (Prediction 1) may have therefore reflected a combination of elevational declines in the local abundances of wood-nesting bees and wasps and the increasing dispersal distances from below-treeline populations. Nevertheless, regardless of the natal origins of the occupants, our trap-nest occupancy data still provide evidence that wood-nesting bees and wasps are capable of accessing sites beyond the treeline and successfully provisioning nests.

In principle, elevational declines in the local populations of wood-nesting bees and wasps could be driven by changes in any variable that covaries with elevation and distance to treeline, which may or may not include nesting substrate. For example, the cooler temperatures and shorter snow-free periods at higher elevations may result in greater rates of offspring mortality if larvae are unable to develop sufficiently prior to the onset of winter (Wong and Forrest 2021). Brood loss from moisture-loving pathogens may also increase with elevation since higher-elevation sites are typically snow-covered (and thus water-logged) for longer periods of time (Westreich et al. 2023), even when daily air temperatures begin to warm (personal observations).

While the elevational declines we observed in the abundances of wood-nesting bees and wasps during insect surveys may indeed be influenced by these factors, they should apply similarly to all bees and wasps, regardless of nesting habit. In other words, elevational changes in the local abundances of wood-nesting bees and wasps should be similar to those of ground-nesting bees and wasps. This was not the case in our study: wood-nesting bees and wasps declined more strongly with increasing elevation than did ground-nesters (Prediction 3). The results of our insect surveys were consistent with the findings of Hoiss et al.(2012), the only other study we are aware of that documented elevational changes in bee

communities with respect to their nesting habits. Although ground-nesting bees and wasps may also experience some degree of nesting substrate limitation due to declines in soil depth with increasing elevation, the abruptness with which the availability of wood declines beyond treelines likely imposes a much stronger constraint on the ability of wood-nesters to establish at higher elevations.

3.5.2 Niche specialization & vulnerability to environmental change

The pronounced disparity we observed between the abundances of wood-nesting and ground-nesting bees and wasps in our surveys, regardless of elevation, reflects the dominant nesting strategy among bees and wasps: ground-nesting is estimated to characterize at least 64% of all bee species (Cane and Neff 2011). Proportions of ground- to wood-nesting species in wasps are similar but have not been formally estimated (O'Neill 2001). Ground-nesting is considered the ancestral condition among these insects (Michener 1964), but one may ask why wood-nesting has remained relatively rare. Having specialized niche requirements may restrict the types of habitats within which species can successfully establish, potentially compromising their ability to respond adaptively to environmental changes in their current habitats. A meta-analysis by Williams et al. (2010) found that bee species that nested in pre-existing cavities responded more negatively than other bee guilds to disturbances such as habitat loss, agricultural intensification and fire, suggesting that the nesting habits of bees affect their capacity to respond adaptively to environmental change. Incidentally, wood-nesting bees are more frequently introduced, accidentally or as managed species, presumably because nests in wood are more easily transported than nests in the soil (Russo 2016). Wood-nesting bees are also thought to be less negatively impacted by urbanization due to the preponderance of cavities found in human-made structures (Fortel et al. 2014). Thus, despite having specific habitat requirements that may not be present in all environments, wood-nesting bees and wasps could be more responsive than ground-nesters to human-assisted conservation efforts.

Our data suggest that the need for wood nesting substrate may limit the extent to which wood-nesting bees and wasps can respond adaptively to climate via upward range shifts. The persistence of these populations as temperatures continue to rise in our study area may therefore depend on their ability to respond in situ. Heritable intraspecific variation in traits such as thermal tolerances or diet breadth may allow populations to persist at lower elevations despite potentially increasing levels of physiological stress and drought-induced declines in food availability (Wong et al. 2025). Nesting females may also be able to behaviourally mitigate the effects of high temperatures by exploiting both spatial and temporal microhabitats—for instance, by occupying more densely-vegetated meadows or by shifting their foraging activity to cooler periods during the day (Bennett et al. 2015). In principle, short-term persistence of these

populations at lower elevations via any in-situ adaptive responses could allow time for local treelines to shift upwards, perhaps reducing the degree to which the lack of wood constrains upper-elevational range limits in the future. However, previous work in our study area has shown that treeline elevations have not advanced upslope over the past century despite significant warming (Sakulich 2015)—a pattern that parallels the findings of numerous studies on treelines in other regions of the world (Harsch et al. 2009). Shifts in local treelines therefore seem unlikely to attenuate nest substrate limitation at high elevations for the wood-nesting bees and wasps in our study system.

3.5.3 Other range-limiting factors

Although our results suggest that the wood nesting bees and wasps at our sites may be limited by the lack of nesting substrate, we cannot conclude that this is the *only* variable preventing upward range shifts in the taxa we observed. Indeed, given the observational nature of our study, we cannot exclude the potential range-limiting roles of other variables specific to wood-nesting bees and wasps in addition to the presence of dead wood. For example, our study species may require not only dead wood but also the presence of wood-boring taxa to produce cavities within the substrate (e.g., wood-boring beetle larvae). The capacity of wood-nesting bees and wasps to occupy beyond-treeline sites would therefore depend additionally on the capacity of these wood-boring taxa to shift their ranges. Obligate relationships with other organisms could also explain why wasps were never observed occupying trap-nests at the four highest-elevation sites in our study and were generally rare in our trap-nests despite being frequent occupants of trap-nests at lower elevation sites (Forrest and Thomson 2011). The wasp occupants in our trap-nests provisioned their nests with lepidopteran larvae and aphids (personal observations), the abundance of which may have become increasingly limiting at higher elevations (Nelson et al. 2019). Determining the range-limiting roles of interspecific relationships with other species such as wood-boring insects and wasp prey would require a better understanding of the capacity of these taxa to shift their ranges—a challenging undertaking given their specific taxonomic identities are unknown, and the lack of basic natural history information concerning their dispersal capacities, habitat requirements and thermal tolerances. Certain wood-nesting taxa may also have additional habitat requirements beyond the presence of cavities in dead wood. For example, wood-nesting wasps in the genus *Passaloecus* employ resin from coniferous trees as nesting wall material (Iwata 1976) further restricting species in this genus to habitats containing a specific form of woody growth. Presumably, the *Passaloecus* occupants observed in our trap-nests were able to access resin either by flying back to treeline, or from krummholz growth present near the sites; however, the fact that we only observed three nests of this genus at our sites and that all were constructed at lower-elevation sites (3479–3503 m) suggests that the lack of nest-construction material may impose an

additional constraint for members of this genus. (Additional comments on *Passaloecus* are in Appendix F).

3.6 Conclusion

Several studies have documented associations between the local abundances of bees and wasps and their habitat requirements, specifically with respect to their nesting habits (e.g. Hoiss et al. 2012, Westerfelt et al. 2015); however, the implications of these findings in the context of climate change have been little explored. Our study suggests that the lack of nesting substrate may play an important role in preventing the wood-nesting bees and wasps in our study system from establishing at beyond-treeline sites, potentially compromising their capacity to respond to rising temperatures by shifting their ranges to higher elevation sites. Observational studies that characterize the roles of habitat requirements and other non-climatic variables in limiting species ranges at local spatial scales, and for targeted subsets of organisms, are important complements to predictions of ranges generated by species distribution models (Lawlor et al. 2024)—especially in the development of major conservation initiatives such as the delineation of protected areas and assisted migration. Ultimately, regardless of climatic suitability, species establishment in any new habitat will be unsuccessful if they lack essential habitat requirements—variables that often require in-situ observation to identify. This study highlights the important contributions of local-scale studies in evaluating the capacity of species to shift their ranges. We also emphasize the importance of basic natural history knowledge, without which we would not be able to identify these variables in the first place. We underscore the need for more studies that characterize the natural history traits of organisms in their natural environments such as their dietary preferences, nesting requirements, interspecific interactions, and dispersal abilities. Such information remains unknown for many taxa yet has the potential to significantly impact their ability to respond adaptively to environmental change.

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Chapter 4

Urban microclimates and the temperature-size rule: juvenile development in urban cavity-nesting bees and wasps

This chapter is in preparation for submission (as of April 2026).

The supplementary material associated with this chapter are in Appendix D.

I conceived of the research ideas for this chapter in 2020 during the COVID-19 lockdowns which prevented travel to Colorado for fieldwork. Dr. Jessica Forrest helped me further develop and refine the research goals. Dr. Illona Naujokaitis-Lewis from Environment Climate Change Canada also helped with the development of research goals and with the procurement of equipment. I conducted field work independently with the support of many dedicated community partners and individuals listed in the Acknowledgements for this chapter. Student volunteers, Kristen Huang, Kirsten Harper, and Pankti Patel assisted data processing (nest dissections and data entry). I wrote the code to analyze the data, generated figures, interpreted the data and drafted the manuscript with the guidance of Dr. Forrest and Dr. Naujokaitis-Lewis.

4.1 Abstract

A common response to elevated temperatures in juvenile insects is accelerated growth and developmental rate, resulting in smaller body size in adulthood (“temperature–size rule”). Given the consequences of reduced body size for individual fitness, elevated temperatures during development may have important implications for the success of insect populations. Urban areas typically exhibit significantly higher average temperatures relative to surrounding rural areas, yet there can also be considerable thermal heterogeneity within cities at smaller spatial scales where local temperature conditions may deviate from landscape-scale means. This small-scale thermal heterogeneity is typically produced by microhabitat features such as vegetation, pavement, and water features. The presence of these local microclimates may allow heat-sensitive insects to persist in otherwise climatically-unsuitable environments. Over three summers, across 31 urban gardens in Ottawa, and Toronto, Canada, we quantified the relationship between juvenile body mass in cavity-nesting bees and wasps and the temperatures they experienced in artificial nesting structures during development. We also characterized the extent to which nest temperatures reflected average landscape-scale thermal conditions and assessed the role of the local microhabitat (vegetation height) in moderating this relationship. Although our data suggested negative responses to temperature for most taxa, mean summer nest temperature was, overall, a weak and non-significant predictor of juvenile mass. Landscape-scale temperature (1 km land surface temperature) was a strong determinant of nest temperature; however, increasing local vegetation height within a metre of nesting structures reduced the strength of this relationship to some extent. Our study highlights the importance of studying insects at juvenile life-stages under natural environmental conditions and characterizes the relationship between landscape climate conditions and microclimates as experienced by small-bodied organisms in urban areas.

4.2 Introduction

Organisms inhabiting urban areas may face unique environmental stressors such as high levels of pollution and soil compaction; more frequent interactions with non-native competitors, predators, or pathogens, poor habitat connectivity, and warmer average temperatures, especially in more highly urbanized regions (reviews in Gaston 2010; McKinney 2006). Among these stressors, the ecological consequences of elevated temperatures may be particularly important given the significant role of temperature as an environmental filter in many ecosystems (Cai et al. 2023, Cabon et al. 2024). Within a city, ambient temperatures in industrial and commercial areas may be 4–5 °C warmer than low-density residential neighbourhoods and urban parks (Rinner and Hussain 2011, Rajagopal et al. 2025). This thermal heterogeneity is primarily driven by large areas of impervious surfaces, reduced evapotranspiration, and heat emitted from traffic, buildings, and industrial activity in highly built-up areas (Yang et al. 2017, Shi et al. 2023). Lower abundances of numerous taxa have been observed in regions of cities characterized by particularly high temperatures (Meineke et al. 2017, Tresch et al. 2019, McGlynn et al. 2019), even after accounting for land-use and resource availability (Hamblin et al. 2018). Moreover, several studies have identified disproportionately negative responses to urbanization among heat-sensitive taxa (Angilletta et al. 2007, Meineke et al. 2017, Hamblin et al. 2017), suggesting that spatial variation in temperature can be an important determinant of a species' capacity to persist in cities.

Although average temperatures may be elevated in built-up areas of cities, structural elements in urban environments can produce distinct microclimates in which small-scale, local temperatures deviate from neighbourhood averages (Chatzidimitriou and Yannas 2015). For example, trees and shrubs may produce cooler or less variable thermal environments within the few metres or even centimetres surrounding them, potentially buffering organisms from negative impacts of elevated or extreme temperatures characterizing the broader thermal environment (Xu et al. 2010, Ziter et al. 2019, Meili et al. 2021). While overall vegetation density in highly built-up regions of cities may be reduced, even isolated trees, shrubs or other vegetation may offer sufficient buffering capacity for certain organisms to persist in otherwise thermally unsuitable habitats (Koenig et al. 2001, Braem et al. 2023). Conversely, buildings, roads, driveways, and other impervious surfaces—typically ubiquitous features of urban environments—can produce relatively hot or extreme microclimates (Chatzidimitriou and Yannas 2015, Wong et al. 2016). Intentionally creating cooler or less variable microclimates by manipulating the built environment may be a practical approach to enhancing habitats for heat-sensitive taxa in urban areas.

Microclimate heterogeneity may have particularly significant consequences for insects (Kerr et al. 2025). Because insects are ectotherms, many aspects of their life-histories such as developmental rate, survival,

longevity and fecundity are highly sensitive to temperature (Bursell 1974, Harrison et al. 2012); however, as small-bodied organisms, they generally respond to environmental conditions at finer spatial scales than those typically represented by landscape averages or even measures of local ambient air temperature (Pincebourde and Woods 2020). Insects in non-adult life-stages may be especially vulnerable to unfavourable thermal environments; for many species, juveniles have limited abilities to behaviourally thermoregulate as they are often confined to a single location or to areas spanning no more than a few metres (Kingsolver et al. 2011). The microclimate conditions characterizing their immediate surroundings (e.g., nest, host-plant, burrow) may therefore be important predictors of their developmental success. A widely documented response to elevated temperatures in juvenile insects is accelerated growth and developmental rate, resulting in smaller body size both in later life-stages and in adulthood (Atkinson 1994, Klok and Harrison 2013). In many animals including insects, body size is a strong predictor of fitness; smaller individuals typically exhibit decreased survival and reproductive output (Kingsolver and Huey 2008). The temperature conditions experienced by developing insects may therefore have important demographic consequences.

The documented responses of insects to elevated temperatures in urban areas are highly variable across taxa and study locations, with respect to both magnitude and direction (Dale and Frank 2014, Youngsteadt et al. 2017, Hamblin et al. 2018, McGlynn et al. 2019, Frank and Backe 2023). Among the taxa that have responded negatively are some species of bees and wasps (Hamblin et al. 2018). The extent to which this pattern is driven by unfavourable conditions for developing brood is unclear. Many studies that examine the relationships between temperature and these insects focus on the responses of entire communities to mean air temperature or landscape-scale averages derived from satellite imagery (Papanikolaou et al. 2017, Soroye et al. 2020, Kammerer et al. 2021, Dejean et al. 2022). These studies help to establish broad associations between species occurrences and average climate conditions, yet the processes underlying the relationships they identify are difficult to decipher based on their results. Characterizing the responses of juvenile bees and wasps to microclimate conditions (i.e., nest temperatures) could provide insight into a possible mechanism that underlies community-level patterns. Moreover, quantifying the extent to which heat-sensitive insects can be buffered from unfavourable landscape thermal conditions through modifications in the built environment (i.e., microhabitat features) may help to inform urban greenspace design, especially given the growing interest in and enthusiasm for wildlife conservation among members of the public (Roll et al. 2021).

In this study, we examine the consequences of microclimate variation in two cities for juvenile bee and wasp developmental success and explore the potential of urban microhabitat features to moderate the

relationship between microclimates and landscape climate conditions. Specifically, our objectives were to: (1) quantify the relationship between nest temperatures and juvenile bee and wasp mass, (2a) characterize the extent to which nest temperatures reflect landscape-scale thermal conditions and (2b) assess the roles of local microhabitat features as moderators of this relationship.

We focused our study on solitary, cavity-nesting bees and wasps. Unlike social species, solitary bees and wasps do not actively thermoregulate their nests, and the period during which their brood are confined to their nests can last anywhere from several weeks to multiple years, depending on the species and habitat (Forrest et al. 2019; Dorian 2024). Most solitary bees and wasps are therefore incapable of avoiding unfavourable temperature conditions for the majority of their lives. Cavity-nesting bees and wasps, which naturally nest in pre-existing cavities aboveground, lend themselves particularly well for observations of juvenile developmental stages. Many cavity-nesting species readily occupy artificial nesting structures which can be placed in locations of interest, thereby eliminating the logistical challenges of finding nests in the field as would be the case for ground-nesting species. Nests constructed in artificial structures can be easily opened to quantify juvenile developmental success in addition to other potential variables of interest such as brood cell production (reproductive output), pollen usage, and parasite attack (Spear et al. 2016, Forrest and Chisholm 2017, Farzan and Yang 2018). Experimental practicalities aside, the developing brood of cavity-nesting species may be particularly vulnerable to unfavourable local temperature conditions as their nests may be more exposed to direct radiant heat and high air temperatures compared to ground-nesting species.

4.3 Methods

4.3.1 Study sites

Data were collected in the summers of 2021–2023 in Ottawa (45.4201° N, 75.7003° W) and Toronto (43.6532° N, 79.3832° W), Ontario, Canada. Both cities are among the most densely populated urban centres in Canada with populations of 1,287,592 (Ottawa) and 3,025,647 (Toronto; Statistics Canada, 2025). Among Canadian cities, Toronto is characterized by particularly intense urban heat island effects (Duan et al. 2024). We established sites in 31 urban gardens—16 and 15 sites in Ottawa and Toronto respectively (Figure S4. 1). All sites were residential gardens except for two which were community gardens (Table S4. 1). In 2021, we solicited volunteers willing to have research conducted on their properties by circulating calls for participation to local community groups in both cities (e.g., gardening clubs, horticultural societies, wildlife interest groups, neighbourhood associations, etc.; listed in the

acknowledgements). We then characterized the mean land surface temperature (LST) within a 1 km radius of each potential site. Land surface temperature was derived from 30 m resolution thermal satellite imagery (band 10 of Landsat 8 and 9, Level-2, Collection 2) retrieved from the EarthExplorer web portal of the United States Geological Survey (Earth Resources Observation and Science Center 2020). Land surface temperature values were obtained by multiplying Band 10 values by a scaling factor and converting values to Celsius (see “Calculating land surface temperature” in Appendix D). Thirty-one sites from the pool of interested participants were selected by iteratively generating sets of sites for each city and selecting the set for which variation in 1 km LST would be maximized and spatial autocorrelation minimized (see “Site selection” in Appendix D). Spatial analysis and LST calculations were performed using functions in the packages “exactextractr” (Baston 2024), “sf” (Pebesma 2018), and “terra” (Hijmans 2025) in R (version 4.4.1). All sites were at least 1 km apart from one another as most solitary bees and wasps forage within this distance (Greenleaf et al. 2007).

4.3.2 Study organisms

Past studies have documented at least 30 cavity-nesting bee and 20 cavity-nesting wasp species in the cities of Toronto and Montreal, the latter of which is 200 km east of Ottawa (Macivor and Packer 2015, MacInnis et al. 2023). Upon mating, females locate nesting cavities, in which they construct a linear series of brood cells, each of which contains a single egg and food provisions, separated by walls consisting of masticated leaves, mud, resin, and/or small pebbles (Krombein 1967, Kierstead 2024). Females may use multiple cavities in succession (Torchio 1989). Nesting phenology varies interspecifically; in our study area, the nesting activity in trap-nests generally begins in April and ends in mid-September (Kierstead 2024).

Upon eclosion, larvae progress through a series of instars during which they consume food provisions, defecate, and spin cocoons before the end of the summer. Some taxa (e.g., *Osmia* spp.) pupate and molt into adults before entering diapause for the winter (Bosch and Kemp 2000), while others overwinter as prepupae (e.g. *Megachile* spp., *Ancistrocerus* spp., *Trypoxylon* spp., *Isodontia* spp.; Cooper 1953, Medler 1967, Kemp and Bosch 2000), and complete development in the following year prior to emergence. In general, the time from egg to cocoon completion occurs over a period of three to five weeks, although timings vary considerably across taxa in addition to being highly temperature-dependent (Cooper 1953, Medler 1967, Torchio 1989, Kemp and Bosch 2000, Scalici et al. 2023). Some taxa (e.g., *Megachile*, *Trypoxylon*) are facultatively multivoltine with a small proportion of offspring (typically those from nests produced early in the season) completing development and emerging in the same year they were born (Tepedino and Parker 1988, Buschini 2007). Our study focused on overwintering individuals.

4.3.3 Trap-nests

In each year of the study, we placed 2–5 trap-nests at each site. Trap-nests consisted of sections of untreated softwood lumber with 10 to 16 tunnels, approximately 14 cm in length. Tunnels were of three different diameters (4 mm, 7 mm, 9 mm) to accommodate a range of cavity-nesting taxa. Trap-nests were mounted either on wooden stakes driven into the ground or on structures found in the gardens (e.g., fences, wooden posts, benches). A wooden or shingle roof was affixed to the top of each trap-nest to protect the contents from the elements. See “Trap-nest design” in Appendix D. The heights at which trap-nests were placed and the directions they faced varied; these variables were documented and later accounted for in analysis. In each year of the study, trap-nests and temperature sensors (see below) were set out in early April and collected from October to November.

4.3.4 Temperature

Nest temperature was characterized using thermocron iButtons (DS1925L-F5# Digi-Key, Inc.; accurate to ± 0.5 °C) placed at the back of each trap-nest, equidistant from the trap-nest roof and base. iButtons were concealed within trap-nests and provided readings every two hours. As with our site selection process, we used land surface temperature within a 1 km radius of each site to characterize landscape temperature conditions for each site using the methods described above (see “Study sites”); however, for the purposes of testing objective 2, we acquired five thermal images per site, per year—one for each month from May to September. Each site was therefore represented by a total of 15 landscape temperature values (3 years * 5 months; but see below). Having multiple measurements of landscape temperature for each site per year allowed for better alignment with the temporal resolution of our measures of nest temperature (see “Data analysis” below). As much as possible, we selected images that had less than 15% cloud cover, and that covered all sites for a given city within the same scene so that imagery dates were the same for a given city-year-month. For city-year-month combinations where there were no scenes that encompassed all sites within the same image and that also had <15% cloud cover, we used multiple scenes; i.e., LST values for that particular city-year-month combination were derived from images captured on different dates. There were also some city-year-month combinations where all scenes were of poor quality (>50% cloud cover); thus, not every site could be represented by 15 LST values in our analyses (Table S4. 2).

4.3.5 Microhabitat

We quantified four microhabitat variables characterizing the environmental conditions directly adjacent to each trap-nest. These included light intensity, the size of nearby water features if present (e.g., fountains, ponds) and their distance from trap-nests, the height and identity of the tallest vegetative growth within 1

m of the nest (maximum vegetation height), and the percent pervious cover of the ground surface within the same 1 m radius (Figure S4. 2). Microhabitat variables were measured on the date of either trap-nest deployment or trap-nest collection (depending on the variable; see Table S4. 3) and were repeated in each year of the study at most sites because the locations of the trap-nests within gardens were not always consistent from year to year. Maximum vegetation height measurements were not recorded for most trap-nests in 2021. Because many of the microhabitat variables were highly correlated with one another and because data were missing or incomplete for some variables, we focused our analysis on maximum vegetation height as a proxy for microhabitat, but present scatterplots of their relationships with nest temperature (Figure S4. 3) as well as their correlations in Appendix D (Table S4. 4).

4.3.6 Nest dissections

At the end of each field season, trap-nests and temperature sensors were brought to a single outdoor location in each city. Developing brood were extracted from their nests in the lab and weighed on a microbalance (accurate to 0.001 mg). Nest wall fragments (e.g., mud, leaves, grass, resin), frass, and residual prey or pollen were cleaned off cocoons prior to weighing (e.g., all leaves from *Megachile* cocoons were removed). All taxa were weighed with their cocoons except for *Passaloecus* spp. and Eumeninae spp. Brood of these taxa were weighed without their cocoons as these taxa had particularly delicate cocoons that we were not able to preserve upon opening nests. In 2021 and 2022, all developing brood were weighed within one month of trap-nest collection. In 2023, weighing occurred over a three-month period. We accounted for the potential effects of water loss over time on cocoon mass by including the day of the year on which each cocoon was weighed in our initial models (see below). Cocoons were overwintered outdoors or in an incubator (see Appendix D). Successfully overwintered individuals were returned to their natal sites the following spring. Taxonomic identities of nest occupants were determined based on a combination of nest construction characteristics (wall material, remnants of prey items, etc.), cocoon morphology, and previous knowledge of the cavity-nesting bee and wasp species that occur in Toronto and Ottawa (Hallett and Darling 2007, Kierstead 2024). Taxonomic identity generally reflected occupant genus but in some cases, subfamily (see groupings in Results). We were aware of there being multiple species within most groupings; however, we were unable to determine exact species identities for all occupants based only on nest and cocoon morphology. Emerged adults from a selection of nests were retained as vouchers—these specimens primarily represented individuals that we failed to release sufficiently soon after they emerged. Vouchers were not systematically retained from all nests due to ethical concerns on the part of homeowners and researchers. Representative photos of the nests and cocoons of each taxonomic group were taken in all years of the study. Vouchers are stored at the University of Ottawa (Forrest Lab), and photos will be archived in

a publicly available repository upon manuscript acceptance. We also recorded the size of the cavity in which the cocoon was found, and noted cases where larvae were found dead or were missing, as well as whether or not brood cells had been parasitized, destroyed by predators (e.g., earwigs, ants, birds), succumbed to mold, or had emerged.

4.3.7 Data analysis

All analyses were conducted in R (ver. 4.4.1.; R Core Team, 2024). We addressed both study objectives using mixed-effects regression models (generalized linear and linear). Model fits were evaluated by visually examining diagnostic plots generated using the “check_model” function in the R package “performance” (Lüdtke et al. 2021). We obtained marginal and conditional R^2 s using the “rsquared.GLMM” function in the R package “MuMIn” and (Bartoń 2020) to evaluate the proportion of variation explained by our fixed and random effects. We also obtained marginal R^2 s to determine the extent to which our main predictors (e.g., nest temperature, LST, vegetation height) explained variation in our response variables by running univariate models with one predictor of interest at a time and all random effects retained. The “emmeans” function was used to generate effect sizes based on model predictions (Lenth and Piaskowski 2025).

4.3.7.1 Objective 1 - relationship between microclimate conditions and juvenile body mass

To evaluate the relationship between bee or wasp mass and mean summer nest temperature, we used a generalized linear mixed-effects model, fitted with the “glmmTMB” function (Brooks et al. 2017) with gamma error distribution (to accommodate skewed continuous data confined to positive values; Bolker, 2008). Each observation in this model represented one cocoon. Mean summer nest temperature was the average between May 24th and September 17th in each year. These dates reflect the latest and earliest dates on which sensors were deployed and collected from the field respectively across all years of the study and correspond to the period during which bees and wasps were actively observed nesting. Mean summer nest temperature was mean centred to improve interpretation of coefficients. Brood cell position within the linear series of cells in the nest was included as a covariate because cavity-nesting bees and wasps typically lay female offspring—which are larger than males—at the back of nests, furthest from nest entrances (Krombein 1967). Brood cell position was scaled to a value between 0 and 1 for each nest. We also accounted for the size of the trap-nest cavity (3 levels; large, medium, and small) as a proxy for species identity, but also because cavity diameter can influence cocoon mass even within species (O’Neill et al. 2010, Seidelmann et al. 2016). However, we note that cavity diameter is an imperfect proxy for species identity, given that in some genera, different species can occupy cavities of multiple sizes (personal

observations). Additional covariates in our initial model included the year in which the brood cell was constructed (3 levels), the day of year on which each cocoon was weighed (scaled to mean = 0 and standard deviation = 1), as well as the city (2 levels) and design of the trap-nest (2 levels) from which the cocoon originated (see “Trap-nests” in Appendix D). All of these terms were removed from the final model as their effects were non-significant. The unique identities of the nest (cavity), trap-nest, and site from which the cocoon originated were included as nested random effects since there were multiple cocoons per nest, multiple nests per trap-nest, and multiple trap-nests per site. In some sites, trap-nests were moved between years in an effort to increase occupancy rates; trap-nest identity was therefore coded as a year-specific variable. We allowed for taxonomic variation in body size and responses to temperature by including taxonomic identity as a random intercept and slope effect. We included the random intercept and slope effects of taxon as separate, uncorrelated terms because including their correlations caused convergence failures (as in Brown, 2021).

4.3.7.2 Objective 2 - relationship between environmental variables

To evaluate the relationship between temperature conditions across spatial scales and the potential role of microhabitat features in moderating this relationship, we used the “lmer” function in the package “lme4” (Bates et al., 2015) to run a linear mixed effects model with land surface temperature, maximum vegetation height, and their interactive effects as predictors for nest temperature. We used the “lmerTest” package (Kuznetsova et al. 2017) which uses Satterthwaite-approximated degrees of freedom to evaluate the significance of fixed factors. Land surface temperature was mean centred to facilitate coefficient interpretation, and maximum vegetation height was square-root transformed to reduce the influence of extreme values. We checked for multicollinearity by examining the correlation between LST and maximum vegetation height and calculating variance inflation factors. The correlation between LST and maximum vegetation height was very weak ($r = 0.06$) and variance inflation factors for all other variables were low (maximum = 1.04). The temporal resolution of our temperature variables differed between landscape temperature and nest temperature; landscape temperatures were represented by the mean land surface temperature at each site on select days of the year (see “Temperature” in Methods) while the iButtons provided bi-hourly records of nest temperature throughout the summer. We therefore calculated daily mean nest (iButton) temperatures for the specific dates represented by the landscape temperatures and used these values to examine the relationship between temperature at different spatial scales (i.e., there were five datapoints for each trap-nest at each site in each year of the study; one for each month from May to September; see schematic in Figure S4. 4). We did not average nest temperatures across all trap-nests in a given site and year, as trap-nests were characterized by different microhabitat characteristics even with the

same site. We included the month of the temperature record as a linear and quadratic term (both scaled to mean = 0, and standard deviation = 1), as well as the height of the trap-nest above the ground, the direction (8 levels; North, Northeast, Northwest, South, Southeast, Southwest, East, West), city, year and trap-nest design as covariates. The unique identity of the trap-nest nested within site was included as a random intercept effect. There was no effect of city, trap-nest height, or trap-nest direction on nest temperature in our initial model so these terms were removed from our final model.

4.4 Results

We observed a 22.9 °C range in landscape-scale temperature conditions (averaged across all LST observations from May to September), from 19.3 °C at the coolest site in one summer to 42.2 °C at the hottest site in another summer. Certain months in some years, (mostly in Toronto) were particularly warm (e.g., May 2022; Figure S4. 5); however average summer air temperatures from May to September were at or near 30-year-averages in all three years of the study based on local weather station data (Table S4. 6). Mean summer nest temperatures averaged over all bi-hourly records from May 24 to September 17 in each year ranged from 18.6 °C to 24.4 °C across all trap-nests. Maximum vegetation height within 1 m of trap-nests ranged from 0 cm to 550 cm (mean = 164 cm).

Across all sites, 274 trap-nests were deployed over the course of the study. Of these, 170 (62%) were occupied by at least one nesting bee or wasp. Of the 874 nests we retrieved from the trap-nests, 71% were constructed by bees, and 29% by wasps. Bee occupants included species in the genera *Osmia*, *Megachile*, and *Hoplitis* (Megachilidae). Wasp occupants included *Isodontia mexicana* (Sphecidae), species in the genera *Trypoxylon* and *Passaloecus* (Crabronidae), and species in the vespid subfamily Eumeninae (likely *Ancistrocerus* and *Symmorphus*). The most common occupants were *Megachile* spp. and *Osmia* spp., who constructed 40% and 30% of nests respectively. Together, all nests contained a total of 4400 brood cells. Of these cells, we were able to extract and weigh 2801 (64%); the remaining 36% were not weighed because either the individual had succumbed to mold, predators, parasites or unknown causes; or the occupants had emerged before nest collection.

Objective 1:

Despite some apparent associations between summer nest temperature and juvenile mass for individual taxa, the global association between nest temperature and juvenile mass across all taxa was weak and non-significant (Figure 4.1; $\beta = -0.03$, SE = 0.07, Z = -0.36, p = 0.72; in the full multivariate model which included covariates such as cavity diameter and cell position). To assess the explanatory power of nest

temperature in isolation, we examined the univariate relationship between nest temperature and juvenile mass; in this model, nest temperature explained a negligible proportion of the variance in juvenile body mass (marginal $R^2 = 0.001$). Marginal and conditional R^2 values for the full model indicated that most of the variance in juvenile mass was attributable to the random-effects structure (marginal $R^2 = 0.07$; conditional $R^2 = 0.92$). Within the random effects, the taxon-level random intercept accounted for 73% of the random-effects variance in body mass (Table S4. 7), whereas the random slope of temperature accounted for approximately 3%.

Objective 2:

The interactive effect of land surface temperature and maximum vegetation height was a significant negative predictor of mean daily nest temperature (Land surface temperature * vegetation height interaction: $\beta = -0.006$, $SE = 0.002$ $df = 1113.5$, $t = -2.53$, $p = 0.01$); visual inspection of the interaction suggested that although land surface temperature was a strong positive predictor of nest temperature, higher maximum vegetation height reduced the strength of this relationship (Figure 4.2a). Land surface temperature still explained a much larger proportion of the variation in nest temperature compared to maximum vegetation height (marginal $R^2 = 0.63$ for LST, marginal $R^2 = 0.002$ for maximum vegetation height) and visual inspection of the interaction with LST as the moderator instead of maximum vegetation height (Figure 4.2b) suggested that even at the highest vegetation heights within the range of values observed, trap-nests in sites characterized by high LST were always warmer than those in cool LST sites.

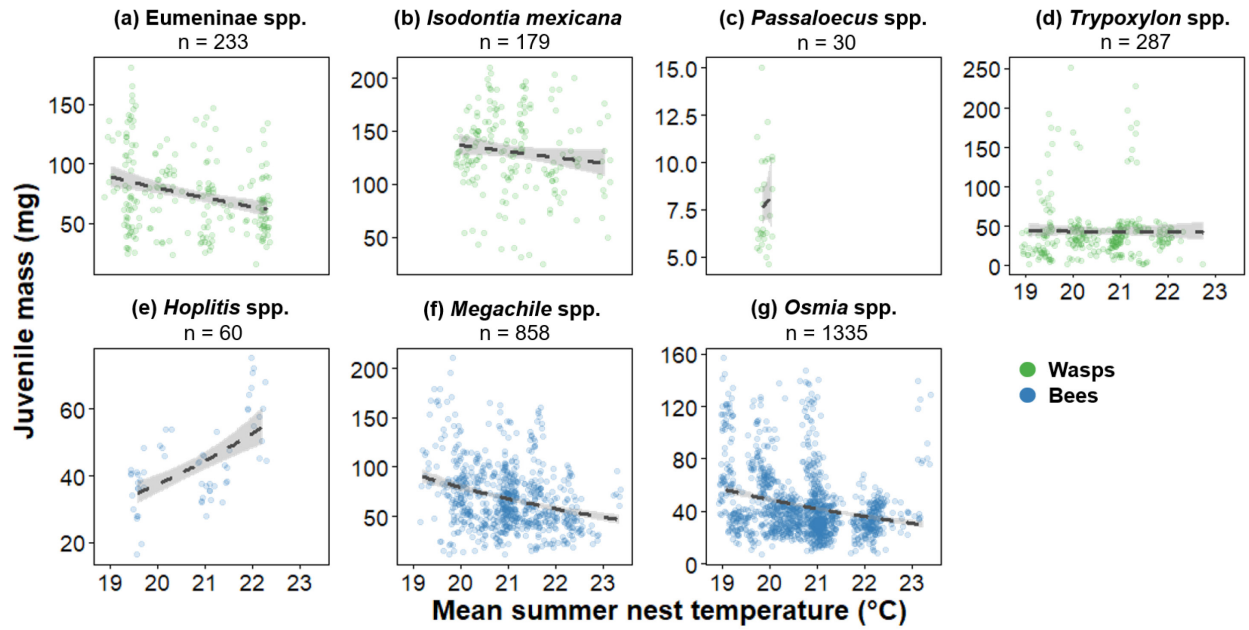


Figure 4.1. Juvenile mass vs. summer nest temperature.

Juvenile mass (mg) as a function of mean summer nest temperature for seven cavity-nesting bee and wasp taxa in 170 trap-nests deployed in 31 urban gardens from 2021 to 2023. Nest temperatures reflect bi-hourly records averaged from May 24 to September 17 captured by iButtons placed within each trap-nest. Each datapoint represents one juvenile bee or wasp. Bands indicate 95% confidence intervals for the slope of simple generalized linear models with log-gamma error distribution. Dashed lines denote the non-significant relationship for the multivariate model described in the main text which included all taxa in the same model. Marginal $R^2 = 0.001$ for a univariate model with mean summer nest temperature as the sole predictor (the main model used to address Objective 1 was a multivariate model that included nest cavity diameter and cell position as additional covariates). Datapoints were jittered for visualization purposes.

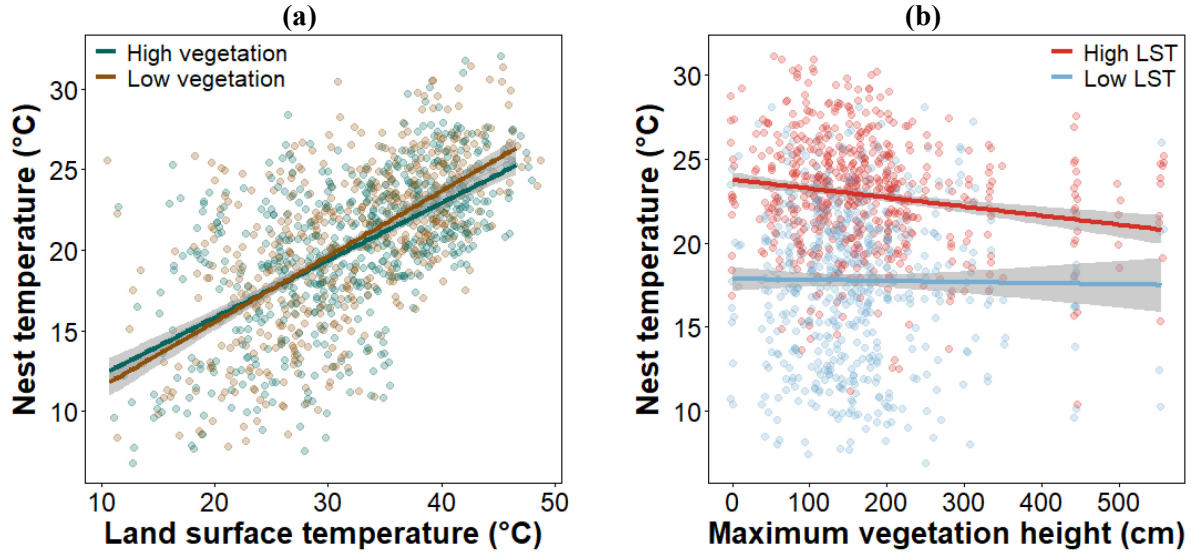


Figure 4.2. Nest temperature vs. landscape temperature and vegetation height.

Daily mean nest temperature as a function of (a) 1 km land surface temperature for the same month and day, and (b) maximum vegetation height within a 1 m radius of the trap-nest. Each datapoint represents daily mean temperature inside a trap-nest for a single day of the year. For (a), data were divided into two equal categories based on maximum vegetation height (greater than and less than the median vegetation height (150 cm), respectively) to visualize the interactive effects of LST and local vegetation. The slope characterizing the relationship between LST and nest temperature for trap-nests with low vegetation height (brown line) is steeper than that of trap-nests with high vegetation. For (b) Data were divided into two equal categories based on median 1 km land surface temperature (LST greater than or equal to, and less than, 33.26 °C respectively) to visualize the interactive effects of LST and local vegetation. The line characterizing the relationship between vegetation height and nest temperature for trap-nests in high LST areas (red line) shows a more appreciable effect of increasing vegetation height on nest temperature than that for trap-nests in low LST areas. $n=1337$ (274 trap-nests; 5 datapoints per trap-nest, 1 value for each month from May to September, except for cases where thermal imagery were not available; See Table S4. 2). Nest temperatures were recorded using thermocron iButtons inserted into trap-nests and land surface temperature was derived from thermal imagery. Bands indicate 95% confidence intervals for the slope of simple univariate linear models. Datapoints were jittered.

4.5 Discussion

4.5.1 Effects of temperature on juvenile development

Over three summers, we characterized temperature conditions inside the nests of cavity-nesting bees and wasps in 31 urban gardens and examined the relationship between juvenile body mass and nest temperature. In general, juvenile body mass tended to decrease with increasing mean summer nest temperature, particularly in the most well-represented taxa; however, the overall (global) effect of temperature across all taxa was weak and not a strong predictor of juvenile body mass.

One possible explanation for the weak relationship between nest temperature and juvenile body mass in our study is that the thermal conditions in the field may not have been sufficiently high to elicit a detectable response. Radmacher et al. (2010) showed significant declines in juvenile body mass of *Osmia bicornis* after 13–17 weeks of incubation in the lab at a constant 28 °C or 30 °C compared to 25 °C. In our study, in which developing brood were subject to natural daily temperature fluctuations, mean summer nest temperatures never exceeded 25 °C (median = 21.5 °C). However, our temperature predictor represented conditions averaged over an 18-week period (mid-May to mid-September) even though larval development would have occurred only during a portion of that period. Developing brood could have therefore experienced warmer or more extreme conditions during their period of active development, depending on the specific timing of nest initiation. We were unable to tailor the temporal window of our temperature predictors to periods of active larval development for each brood cell as trap-nests were not monitored during the field season, and nests would have been constructed through the entire season.

Related to this, developing bees and wasps may respond more strongly to shorter periods of high temperatures at or near their thermal optima (heatwaves), or to pulses of extreme temperatures for a few hours beyond lethal limits (heat shocks) during development rather than average conditions. That said, while these forms of thermal stress have been shown to impact larval mortality and protein expression, their consequences for juvenile body mass specifically remain unclear. Interestingly, while a small proportion of trap-nests may have reached more extreme conditions (e.g., >35 °C for several hours in a day for multiple days), many of these trap-nests remained unoccupied (data not shown), suggesting that nesting females may have preferentially nested in cooler trap-nests—a behaviour that has been documented in a number of studies (Hranitz et al. 2009, Wilson et al. 2020, Ostap-Chec et al. 2021).

4.5.1.1 Other responses to temperature

It is also possible that the taxa in our study simply do not conform to the temperature-size rule. Numerous studies have documented shorter development times in cavity-nesting bee larvae exposed to warmer temperatures (Whitfield and Richards 1992, Kemp and Bosch 2000, Radmacher and Strohm 2011, McKinney et al. 2017, Scalici et al. 2023); however, for the most part, it is unclear whether these changes in development rate also led to changes in body size prior to diapause. Among the few studies that captured the effects of temperature during larval development for both development rate and pre-diapausal body mass, evidence for the temperature-size rule is mixed. Radmacher & Strohm (2011) showed both decreased development time and decreased body mass with increasing temperature in *O. bicornis*—results which support the temperature-size rule (albeit with relatively extreme temperature treatments). Meanwhile, Melone et al. (2024), who exposed the developing brood of *Osmia lignaria* to heatwaves under realistic

diel cycles, found significantly reduced development time, but no effect on body mass, suggesting that accelerated development does not always result in body mass reductions. Importantly, Melone et al. (2024) found significantly increased mortality at their highest temperature treatment (37 °C), with most mortality occurring during the egg and first instar stages—a result that has been reflected in a number of other studies that have also suggested higher temperature sensitivity at the earliest developmental stages (Hranitz et al. 2009, Song et al. 2023). We did not examine the relationships between nest temperature and mortality in our study; however, it is possible that in trap-nests characterized by warmer temperatures, eggs and/or early-instar larvae died, and our study captured only the effect of temperature during less-sensitive, later developmental stages for individuals that survived.

4.5.1.2 Other determinants of juvenile body size

Our findings for Objective 1 could also reflect the fact that juvenile body size in developing bees and wasps can be influenced by many other variables apart from temperature which were unaccounted for in our study but that are generally held constant across temperature treatments in lab experiments. For example, several studies (Danforth 1990, Bosch and Vicens 2002, 2005) have documented strong positive relationships between body size and provision volume, which may in turn depend on factors such as the local availability of food resources and maternal condition (e.g., body size, age, wing wear etc.). Other documented drivers of juvenile body size in bees and wasps include provision quality (e.g. protein content in bee pollen provisions; Roulston and Cane 2002, Radmacher and Strohm 2010), genetics (Pinto et al. 2015, Yu et al. 2023), and humidity (May 1972). All of these variables could have contributed to juvenile body mass, making the effects of temperature difficult to detect. It is also possible that the relative importance of these other variables in driving variation in body mass is greater when temperature conditions are mild, as in our study.

4.5.1.3 Inadequate taxonomic resolution

We also acknowledge that our relatively coarse taxonomic resolution (based primarily on genera and not species) likely also contributed to the lack of relationship observed between nest temperature and juvenile mass. Congeneric species in our study area certainly differ with respect to baseline body size (Normandin et al. 2017) and may also differ in their responses to temperature (Hamblin et al. 2017); however, our model would not have been able to parse the variation in body mass attributable to interspecific differences within the taxonomic groups we used. We note that the inclusion of cavity size in our models should have accounted for some variation in body size across congeneric species but also recognize the inadequacy of

this proxy given that conspecifics may still nest in different-sized cavities (Strickler et al. 1996, Pizzini et al. 2025).

4.5.1.4 Body mass for most genera decreased with increasing temperature

Notably, despite the coarse taxonomic resolution, our results suggest appreciable taxon-specific responses to temperature. Specifically, a post hoc likelihood-ratio test suggested that including the taxon-specific random slope term for nest temperature significantly improved model fit compared to the intercepts-only model ($\chi^2 = 17.0$, $df = 1$, $p < 0.001$, $\Delta AIC = 15$). Taxon-specific slopes predicted by the model as well as visual inspection of Figure 4.1 suggest that body mass declined with increasing temperature for most taxa. We note that the slopes for two out of the three taxa that apparently responded positively to warmer temperature (*Hoplitis* and *Passaloecus*) are likely not biologically meaningful given their limited representation in the dataset and the narrow range of temperature conditions they occupied (both taxa were only observed at four sites and in a single year). Qualitatively, the overall effect of warmer nest temperature on body mass was therefore negative for most taxa, although we may have been unable to detect a stronger signal due to a combination of the reasons outlined above. This finding, in addition to the high sensitivities of eggs and early instars to unfavourable temperatures suggested by other studies, suggest that nest microclimate conditions, and the environmental variables that influence them may still have important consequences for the developmental success of cavity-nesting bees and wasps.

4.5.2 Relationships between environmental variables

Our findings for objective 2 suggest that nest temperatures were mostly determined by the thermal conditions of the broader landscape; however, our data also suggested that the strength of this relationship was moderated by local microhabitat features. Specifically, the slope of the relationship characterizing the effect of landscape-scale temperature on nest temperature decreased slightly as maximum vegetation height increased. The contribution of vegetation to local microclimate buffering in cities both through shading effects and through evaporative cooling has been well-documented (Xu et al. 2010, Ziter et al. 2019, Meili et al. 2021). Even small patches of vegetation can generate cooler conditions directly within their vicinity (Dimoudi and Nikolopoulou 2003).

Our results suggested that cooling effects of increasing vegetation were only apparent in sites and on days characterized by high LST. This pattern could have arisen because the presence of vegetation in parts of the city characterized by high LST likely represented a more significant deviation from the average environmental conditions characterizing the broader region (i.e., low vegetative cover, high impervious

surface area). At the highest landscape temperature conditions (46.6 °C in July), model predictions suggested that daily mean nest temperature in trap-nests near trees (e.g., maximum vegetation height = 550 cm) were nearly 3 °C cooler than trap-nests without any vegetation within 1 m of them (27.7 °C compared to 30.6 °C). While an increase in maximum vegetation height from 0 to 550 cm resulted in a 3 °C difference in nest temperature when landscape temperature conditions were at their highest, the overall buffering effect of vegetation was modest; nest temperature increased by 0.52 °C for every 1 °C degree increase above the mean LST (32 °C) when vegetation height was 550 cm compared to 0.65 °C when there was no vegetation (maximum vegetation height = 0 cm) for the same LST increase. That said, vegetation may offer other benefits to bees and wasps apart from thermal buffering such as food provisions for nesting females. We also note that although vegetation height alone may not have had a strong influence on nest temperature, other microhabitat elements such as the presence of water features and properties of the ground surface (e.g., pervious vs impervious) may operate additively to produce microclimates that deviate more strongly from landscape-scale climate conditions.

4.5.3 Conclusion

Many ectotherms have been found to conform to the temperature-size rule, reaching smaller body sizes when reared in warmer temperatures. While there may have been some indication of this pattern for certain taxa in our study, we did not detect a strong global relationship between juvenile body mass and summer nest temperature. In addition to the possible biological and methodological explanations for this result, this finding may also reflect the fact that observational studies are somewhat constrained to the organisms that are naturally present in the area, which by definition, are often those that can tolerate the local conditions. While cities may exhibit warmer conditions on average compared to surrounding rural or less-developed areas, the organisms inhabiting them may also be characterized by higher thermal tolerance. Indeed, urban biotic communities are often found to be dominated by thermophilic species (Angilletta et al. 2007, Hamblin et al. 2017, Cabon et al. 2024).

Nevertheless, given that climate projections for Ottawa and Toronto include significant increases in temperature means and extremes within the next decade (National Capital Commission et al. 2020, Lam et al. 2024), the extent to which our focal taxa—even those that are seemingly heat-tolerant—can persist remains unclear. Our study suggests that the local microclimate conditions experienced by small-bodied immobile insects are strongly determined by landscape-scale climate conditions. Mitigating any negative impacts of high or extreme temperatures may therefore require relatively large-scale initiatives, such as the incorporation of green and blue infrastructure (e.g. semi-natural areas, parks, inland ponds and wetlands;

Hu & Li, 2020; Kumar et al., 2024; Marando et al., 2022). The implementation of large-scale infrastructural changes can often be slow in cities due to lengthy approval processes and the need to coordinate between multiple stakeholders. Nevertheless, our findings also suggest that efforts occurring at the scale of a single garden may have small but still measurable buffering effects—especially in particularly warm parts of the city during the hottest parts of the summer. It is therefore possible for the cumulative cooling effects of many small-scale efforts by individuals and local community groups (e.g., planting trees or shrubs), to amount to significant thermal buffering for small-bodied organisms.

4.6 Acknowledgements

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General discussion

When I wrote the proposal for this thesis in 2020, declines in the populations of bees were primarily being attributed to habitat loss, pesticide use, and the spread of pathogens (Potts et al. 2010, Goulson et al. 2015). The demographic consequences of climate change for bee populations were less well-documented (although Kerr et al. (2015) provided some indication, showing significant contractions in warmer parts of species' ranges). It is now 2025, and since then, several large-scale studies have documented changes (or lack of change) in the abundances and distributions of many bee species in response to recent climate change across relatively broad spatial and temporal scales (Soroye et al. 2020, Kammerer et al. 2021, Pardee et al. 2022, Jackson et al. 2022, Kazenel et al. 2024, Quinlan et al. 2025). The population-level responses of wasps to climate change remain undocumented. For bees, responses of taxa have varied across these studies—some species have responded positively over the past few decades in response to warming, while others seem to have shown no response. Nevertheless, all of these studies suggest that the populations of many species—particularly those in regions that have experienced significantly warmer and drier conditions—have declined in recent years, even after accounting for other stressors such as land-use change. The realized and potential negative consequences of climate change for bee (and likely wasp) populations are now apparent. Moreover, although some species have thus far responded positively or neutrally to warming, it remains uncertain whether these trends will persist as conditions become increasingly hot and dry.

Nevertheless, despite the growing recognition of climate change as a potentially significant driver of declines in bee populations (Dicks et al. 2021), the ecological processes that drive these patterns remain unclear. Why have populations declined (or not declined) with warmer temperatures? Why are species distributions shifting, or failing to track changing climate envelopes? What intermediary relationships generate these large-scale patterns? If addressing biodiversity decline is a goal for ecologists, documenting declines in abundance or contractions in geographic range under hot and dry conditions may not suffice. Rather, designing meaningful conservation initiatives may require a deeper understanding of the local-scale processes that drive changes in abundances and distributions (Lyles and May 1987, Green et al. 2015, Westin et al. 2018, Demarse et al. 2023).

This thesis examines some of the local ecological processes that may underlie changes in wild populations of bees and wasps as climate conditions become increasingly warm and dry. Across the four studies it contains, several processes emerge, involving both direct pathways (i.e., driven by changes in climate variables themselves) and indirect pathways (i.e., driven by the effects of climate variation on other variables).

Direct effects of climate variation

The results of Chapter 1 suggest that the consequences of climate change could be driven by the impacts of warming on the longevity of nesting females and the relationship between longevity and reproduction. This finding may point to physiological mechanisms, given the large body of literature linking high temperatures to accelerated oxidative and immune-related stress markers and therefore shortened lifespan in many animals, including bees (Pearl 1928, Sohal 1986, Sgolastra et al. 2011, Hayes and López-Martínez 2021). The strong relationship we observed between foraging temperatures and nesting rate likely also reflects physiological mechanisms given the temperature-dependent nature of functions involved in flight such as muscle contraction and metabolism (Harrison and Roberts 2000). Notably, nesting rate responded positively to warmer temperatures, while longevity (and reproductive success) responded negatively, highlighting the importance of directly quantifying fitness metrics at the level of individuals; had we based our assessment of the consequences of warmer temperature for populations solely on activity metrics such as nesting rate or the number of bees seen foraging, we could have concluded that warmer temperatures benefit high-elevation bee populations when the actual net demographic effect may be negative.

Potential physiological processes are also invoked in Chapter 2, which used structural equation models to characterize causal relationships and identified a direct negative effect of high summer temperature and drought severity on individual brood cell production. This result could be attributed to the negative effects of warmer conditions on physiological processes such as oviposition and oocyte development (Engelmann 1970, Maeta and Kurihara 1971); however, as I discuss later on, extrinsic variables may be implicated here too. Chapter 4 investigated a specific physiological process—namely, accelerated juvenile development resulting in reduced body mass given warmer temperatures during development (Atkinson 1994). The associations between nest temperature and juvenile mass for most taxa were generally negative, although the global effect of warmer temperature across all taxa was not significant.

While these results all suggest that physiological processes likely underlie larger-scale patterns of abundance given climate change, the extent to which they actually contributed to the relationships I observed is unclear because physiological traits (*sensu stricto*) were not measured in these studies and because of the limitations of our observational data (e.g., correlative relationships, unmeasured variables). Nevertheless, the general direction of the responses to warmer temperatures observed across chapters, i.e., reduced brood cell production (Chapters 1–2), and potentially reduced juvenile body mass (Chapter 4), broadly align with well-documented relationships between temperature and physiological traits such as oxidative stress, heat shock responses, oocyte development and metabolic rates (Maeta and Kurihara 1971, Yocum et al. 2005, Sgolastra et al. 2011, Song et al. 2023), which are directly implicated in the response variables we characterized. Future observational studies that directly measure these physiological traits in natural populations and that also link them to fitness parameters could provide more direct evidence for the role of physiological mechanisms in driving larger-scale patterns of abundance. That said, quantifying physiological traits on small-bodied organisms directly in the field may be logistically challenging given the sophisticated lab equipment these measurements often require.

Although the physiological consequences of high temperatures are typically conspicuous in lab settings (e.g. Wieser, 1973), the results presented in this thesis suggest that these relationships may not play out as strongly in natural environments—as evidenced by the wide variance in responses to temperature across individuals in Chapters 1 and 2 (Figure 1.5, Figure 2.3), and the weak global effect of nest temperature in Chapter 4 (Figure 4.1). These discrepancies may have arisen because although bees and wasps are ectotherms and inherently sensitive to temperature, they are also highly capable of behaviourally responding to thermal stress as adults and likely on behalf of their offspring; e.g., by modifying foraging times, avoiding direct solar radiation, or selecting cooler nest-site locations (Willmer & Stone, 1997; Wilson et al., 2020). These behavioural responses ultimately determine what temperature regimes an individual experiences and are challenging or impossible to account for in laboratory settings. While controlled experiments are better able to detect responses to a wider range of conditions (including extreme conditions) and confirm causal mechanisms, observational studies that complement them are necessary both to inform their design (i.e., selecting relevant temperature regimes) and to validate their findings in situ.

Indirect effects of climate variation

Indirect processes mediated by extrinsic factors may also be important in driving the responses of bee and wasp populations to warmer and drier climate conditions. The results of Chapter 2 suggested that population-level declines in bees could be driven by the negative effects of warmer and drier conditions

on floral resource availability. Although relationships between bee abundance and floral resources are well-documented (reviewed in Hyjazie and Sargent 2022), few studies directly link floral resource availability to brood cell production, despite the potential utility of such information for parameterizing predictive models (but see Minckley et al., 1994). Resource availability may also play an important role in mediating relationships between climate and species' geographic ranges. The results of Chapter 3 suggest that the upper-elevational range limits of cavity-nesting bees and wasps are constrained by the availability of suitable nesting substrate at high elevations, which could prevent populations from establishing in climatically suitable habitats even if they are within dispersal distance. Several studies have suggested that the local abundances of cavity-nesting bees and wasps can be limited by their need for dead wood (e.g., Hoiss et al. 2012; Westerfelt et al. 2015). Chapter 3 extends their findings by examining the implications of this habitat requirement for the capacity of these species to respond adaptively to changes in climate and could help to explain why some species fail to shift their ranges following bioclimatic model predictions.

While floral resources and nesting substrate were explicitly examined in this thesis, they are but two of many other possible extrinsic variables that may have been implicated in the responses we observed. Indeed, in the discussion of every chapter, I make note of the potential role of unmeasured variables in mediating the observed effects of temperature (or elevation for Chapter 3) on our response variables. In Chapters 1 and 2, these variables include interactions between the focal taxa and parasites and competitors as well as unmeasured aspects of floral resource availability (i.e., pollen and nectar quality and quantity). In Chapter 3, I acknowledge the potential role of other habitat requirements as well as species interactions in constraining the upper-elevational range limits of the focal taxa (e.g., wood-boring taxa, prey for wasps), and in Chapter 4, I make note of other determinants of juvenile mass (e.g., provision volume and quality, humidity). All of these variables can influence parameters such as reproductive output, nest occupancy, and body size, and in many cases, they are also influenced by climatic conditions. When these variables covary with climate, they may mediate the effects of climate variation on the demographic responses we observed (i.e., they can drive indirect effects). Importantly, these unmeasured variables could also reduce the apparent explanatory power of climate if they act independently of the climate predictors included in our models. The potential influence of such unmeasured variables throughout this thesis—whether climate-mediated or not—reflects a common limitation of observational studies. That said, I also see this limitation as an impetus for greater efforts to characterize the natural history of organisms in their natural habitats, without which the indirect processes linking temperature to population success would be difficult or impossible to identify.

Applications to conservation

In principle, empirical observations that identify the local ecological processes driving climate-species relationships may be able to offer practical information for conservation. For example, population declines driven primarily by drought-induced reductions in floral resources could perhaps be attenuated by increasing floral resource availability. Declines driven by heat- or moisture-related juvenile mortality could potentially be addressed through the creation of cooling microhabitats such as trees or ponds. Of course, these scenarios represent highly simplified examples because implementing such interventions at large scales may not be practical. However, I emphasize here that these distinct ecological processes and their associated demographic responses would warrant different conservation measures; studies that focus on broad associations between climate variation and the abundances and distributions of many species in aggregate would likely obscure them. I also note that along with most bee and wasp species, the conservation status of the specific taxa featured in this thesis are currently all unknown. This certainly does not imply that they do not warrant conservation, as they may indeed be experiencing declines, but only that they may unfortunately not be the focal taxa of formal conservation initiatives in the near future. That said, the findings of my thesis could still provide practical information for informal conservation action initiated by community members at small scales (e.g., neighbourhoods, community organizations), or at the very least, provide the scientific underpinnings to support existing initiatives. More broadly, these studies may also serve as a useful methodological template for other studies with different taxa.

Methodological limitations

Apart from the use of artificial nesting structures, my findings are based purely on observational data. As with any empirical framework, be it controlled experiments or distribution modelling, observational approaches come with limitations with respect to the interpretation and generalizability of their results. For example, one common limitation of observational studies is that relationships between predictors and responses are restricted to naturally-occurring environmental variation which can constrain the possibility of detecting responses to more extreme conditions and/or non-linear responses. This limitation was somewhat addressed in my thesis through the use of multiple sites and multiple years of data in each study. That said, Chapters 3 and 4 certainly did not encompass the full range of historical climate variation over their three-year duration, and even the slightly longer study durations in Chapters 1 and 2 (six and nine years respectively) may not have captured sufficient environmental variability to make strong inferences about the consequences of climate change in this study region (e.g., the relationship between floral density and climate in Chapter 2 was much more apparent in the 45-year flower dataset compared to 9-year dataset). Maintaining long-term ecological datasets may therefore be critical for

understanding and predicting the consequences of climate change for organisms, especially for capturing the responses of populations to extreme environmental conditions which may become increasingly prevalent in the coming years. That said, there may be ways to experimentally increase the climate variation captured by field studies over shorter time periods such that the strengths of an observational approach are still retained (e.g., ecological complexity, natural populations). For example, CaraDonna et al. (2018) manipulated the colour of trap-nests placed in the field such that some were slight warmer than others and examined the consequences of temperature for juvenile development and survival. Others have experimented with placing trap-nests in sunnier or shadier areas or with different orientations (Hranitz et al. 2009).

I also note that although my use of the word “process” throughout this thesis may imply causality, I am aware that the observational nature of these studies means that the relationships I describe are correlational. For example, in Chapter 1, I suggest that short season lengths and cooler early-season temperatures may be driving the seasonal decline in reproductive output; however, it is also conceivable that early nesting, increased longevity, and high reproductive success are all correlated maternal traits and that the activity period of individuals exhibiting these traits happens to coincide with cooler periods of the season. As much as possible, I explicitly acknowledge this limitation in the discussion sections of each study and in Chapter 2, I directly address this limitation by using structural equation modelling—a statistical tool designed to test causal hypotheses (Frauendorf et al. 2021). Experimental manipulation may therefore still be necessary to confirm causal mechanisms, although there are also methodological techniques that allow for causal relationships to be derived from observations of natural populations (Byrnes and Dee 2025).

Apart from limitations that stem from observational data, the findings of my thesis also depend on the extent to which I was able to adequately characterize the environmental conditions experienced by my study organisms. For the most part, temperature sensors were methodically placed to best capture conditions experienced by foraging adults or by developing brood; however, the temporal scales and windows over which the data were averaged may not have always been an accurate reflection of the conditions individuals experienced. Some taxa may respond more strongly to brief periods of high temperatures or temperature fluctuations—aspects of the thermal environment that may be obscured when temperature is averaged over several months. The consequences of unfavourable climate conditions for bees and wasps may also depend on when they occur during an individual’s lifecycle. For example, numerous lab studies have demonstrated that warmer wintering temperatures can strongly impact variables such as body mass, reproductive output and longevity post-emergence (Bosch and Kemp 2003,

Fründ et al. 2013, Schenk et al. 2018b, Müller et al. 2025); however few studies have examined the fitness consequences of winter temperatures for bees and wasps in natural settings.

Implications for further warming

What do these results mean for the bee and wasp populations in these studies in light of the warmer and drier conditions projected for the coming years? Given the generally negative demographic consequences suggested by these results, even within the range of environmental variation captured, further warming and drying is likely only to exacerbate floral resource limitation and physiological stress. For montane cavity-nesting insects, the extent to which populations can respond by establishing at higher elevations may be limited due to the lack of nesting substrate at these sites and the fact that treelines are unlikely to keep pace with the rate at which bees and wasps may disperse. Moreover, warmer temperatures could potentially impair juvenile developmental success, at least in some species (although this was unclear from my thesis).

The persistence of these populations in the face of climate change will depend on their capacity to respond adaptively in other ways. For example, nesting females may be able to shift their foraging activity to cooler parts of the day to avoid stressful daytime temperatures (Maia-Silva et al. 2021) or may be able to choose to nest in more shaded or vegetated areas to protect both themselves and their developing brood from unfavourable climate conditions (Hranitz et al. 2009). Whether these behaviours translate into long-term population persistence will depend on whether or not they are heritable traits as well as the degree to which they actually improve individual survival and reproductive success. Our study system lends itself particularly well to characterizing the heritability of potentially adaptive traits and quantifying the fitness consequences of variation in such traits; cavity-nesting bees have often been observed to nest in similar locations to where they emerged from (i.e., philopatry; Steffan-Dewenter & Schiele, 2005). The correlation between traits expressed by individually-marked females could therefore be linked to traits expressed by their offspring given that they are likely to nest close to where their mothers nested in the previous year. The fitness consequences of variation in such traits could be characterized by examining relationships between these traits and the total brood cell production and/or individual longevity.

The consequences of future climate change may also manifest in population-level shifts in phenology or in distribution, rather than resulting in the extinction of a local population. Selection for nesting even earlier in the season when conditions are cooler may increase; however, whether this results in

phenological shifts at the population level will depend on the heritability of nesting timing and on the extent to which the phenology of floral hosts also shifts. Moreover, in montane habitats, even if the lack of wood nesting substrate is limited at higher elevations, populations may be able to persist at current elevations by occupying north-facing slopes below treeline where conditions are generally cooler and wetter.

Finally, although the findings of this thesis suggest that warmer temperatures had significant negative demographic consequences for the focal taxa, for the most part, the climate variables examined explained little of the total variance in the response variable in question. Marginal R^2 values for the univariate effects of climate variables on individual reproductive output and juvenile mass were generally low (Appendix E: Table S0. 1). I recognize that the methodological limitations of purely observational data likely contributed to the low explanatory power we observed. That said, assuming these methodological limitations did not overwhelm the underlying ecological relationships, the residual variation could also reflect behavioural flexibility (e.g., foraging during cooler times, nest site preferences) and the presence of microhabitats—variables that could buffer the effects of climate such that it only explains a small part of the observed variation in fitness. Ultimately, I cannot disentangle the contributions of these variables from those of the methodological limitations described above. The empiricist in me would like to investigate the role of these variables with further studies that address some of the methodological limitations. The quiet and cautious optimist in me takes some comfort in knowing that some of the residual variation may reflect the resilience of these organisms to environmental stress and their potential to respond adaptively.

Conclusion

It seems that the forefront of research on the ecological consequences of climate change is becoming increasingly dominated by large-scale studies that encompass the climate responses of species across large geographic areas over many years. Many of these studies have identified negative associations between climate change and biodiversity, documenting significant declines in species abundance and/or contractions in geographic ranges under warmer and drier conditions. However, unlike other major global change drivers such as habitat loss—where the causal pathways linking the stressor to biodiversity decline are more immediately apparent—the mechanisms underlying large-scale climate–biodiversity patterns are less clear. A range of intermediary processes may link changing climate conditions to demographic declines, including direct effects on physiology, as well as indirect effects mediated by resource availability, phenology, and species interactions. All of these processes may interact with each other and be influenced by other large-scale environmental stressors. Macroscale studies certainly play a critical role in quantifying the magnitude of the ecological consequences of climate change; however, focusing only on broad patterns can sometimes have the effect of reducing what are highly complex ecological processes to the vague sentiment of “climate change is bad” (or “will be bad”). Meanwhile, questions such as “*why* and *how* is climate change bad?” and “for *whom* is it bad?” remain unclear from these studies, despite the potential for the answers to play essential roles in bridging the findings of macroscale studies to effective conservation.

The recent increase in prevalence of macroscale studies may be largely attributed to advances in data availability and accessibility. It is now much easier to compile large climate datasets alongside occurrence data for many species in aggregate. However, I wonder if the appeal of such studies might also stem from a societal attraction to making broad generalizations about the world, which can often carry more rhetorical significance. While generalized findings certainly have their place with respect to motivating policy and influencing public awareness, they also homogenize the myriad ways in which different species, populations and individuals may respond to climate change. Focusing on individual-level responses with smaller subsets of species allows us to capture this variation and draw more direct inferences about the demographic processes underlying the impacts of climate change. Individual-level data can also reveal intraspecific variation in traits such as dispersal capacity and behavioral flexibility in foraging and nesting—information that could provide a more concrete indication of the capacity of species to respond adaptively. In light of this, my hope is that this thesis highlights the importance of asking what the consequences of global environmental change might look like for individual organisms. Beyond pragmatic applications, my own experience, having completed the writing of this dissertation, is

that individual-level studies bring the researcher to the level of their subjects in a way that fosters a rather unique connection between the human and the non-human. The outcome of this is that the human becomes quite moved to do something concrete about the problem she has quantified because she realizes that she too is one individual—one of 8.3 billion of her species among at least another 8.7 million species.



Jane—the exceptional bee (Brush Creek, Crested Butte, Colorado 2019)

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Appendix A - Chapter 1 Supplementary information

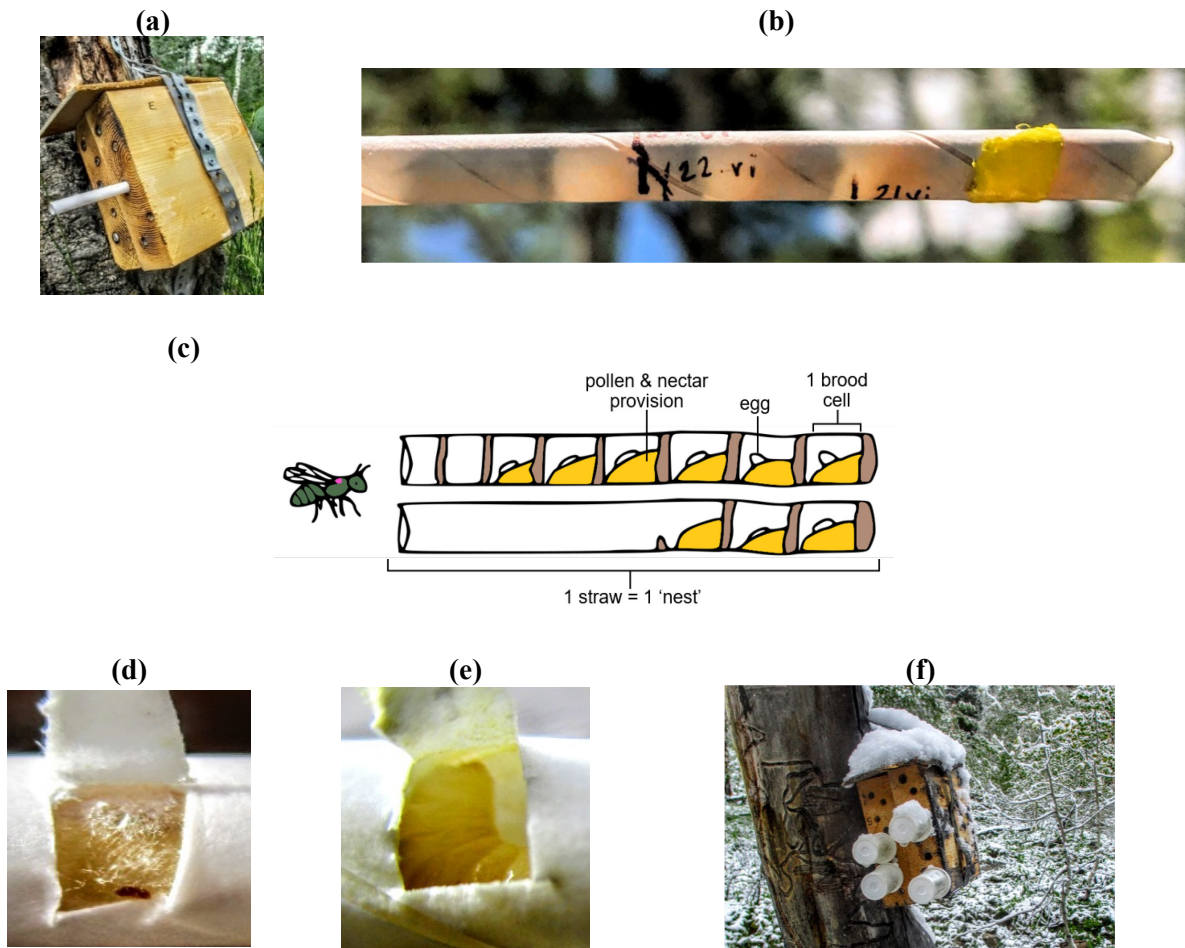


Figure S1. 1. Study design.

(a) Wooden trap-nest attached to tree with one paper nesting-straw partially extracted. Cavities are of three diameters: 4.5, 6.1, and 8.2 mm. (b) Paper straw containing an individual's nest with leading edge of most recent pollen-and-nectar provision marked in pen. This nest contains approximately 3 brood cells. A small window was cut into the straw at the first cell for pollen sampling (see Supplementary methods); straw was subsequently repaired with tape. Note the presence of the mother bee inside the straw to the left of the outermost cell partition. (c) Diagram of nest interior with an individual (marked with pink paint) who has two nests (i.e., she has so far used 2 paper straws throughout her nesting period). Nests consist of a linear series of brood cells each of which contains an egg and pollen provision. We counted the number of eggs produced by each individual across all their nests to determine total reproductive output. This individual's reproductive output is currently 8. (d) & (e) Photos of bee larva that (d) has completed a cocoon, and that (e) has not completed a cocoon. (f) Trap-nest with snap-cap vials to measure emergence. Photo and illustration credit (a, c, d, e, f): LHW. Photo credit for b: Isabel Rivera.

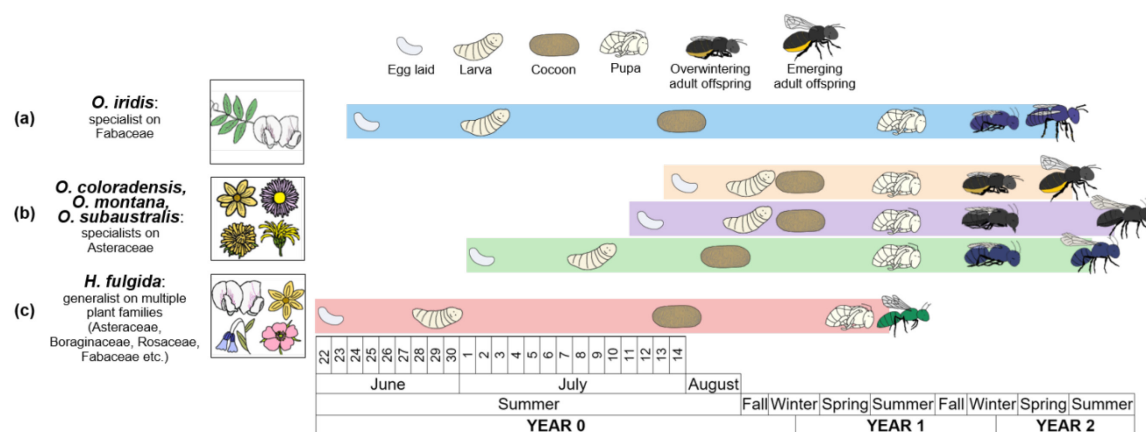


Figure S1. 2. Bee life-history information.

Pollen specialization, lifecycles, and phenologies of five bee species at our Colorado study sites. The placement of the egg stage relative to June and July dates represents the median nest initiation day determined over all sites and years across all individuals of each bee species. The placements of the “larva”, “cocoon”, “pupa”, and “overwintering adult offspring” life-stages are arbitrary as we do not have data on their exact timing. Note the lifecycle difference between the semivoltine *Osmia* species (a, b) and the univoltine *H. fulgida* (c): In (a) and (b), offspring spend their first winters as cocooned late-stage larvae (prepupae), pupate the following summer, and spend their second winters as adults before emerging two years after they were born. In (c), *Hoplitis fulgida* spend a single winter as prepupae in their cocoons, pupate, and emerge the summer after they were born. Most *Osmia* individuals observed at our study sites exhibited the illustrated two-year cycle (90%); however, one-year cycles have been observed on occasion in *O. iridis* (Forrest et al. 2019). To answer Question 1b (*Hoplitis fulgida* only), “larval developmental success” was recorded in year 0 (around the “cocoon” stage), and “emergence success” was recorded in year 1 (around the “Emerging adult offspring stage”).

Methods: Supplementary text

Verifying floral hosts

We verified the floral host-plants used by each bee species by taking pollen samples from the innermost and outermost cells of each completed nest (or, only the innermost cell for nests with fewer than four brood cells). This was achieved by removing nesting straws while females were out foraging or after nests were completed and cutting small windows in the paper straws so that a sample of pollen from the brood cell could be collected using fine forceps. Straws were repaired with tape and re-inserted into the nesting blocks (Figure S1. 1b). Pollen samples were then melted on a microscope slide with fuchsin stain, examined under a compound microscope, and compared with a pre-existing local reference collection to determine their identity, to family or genus level (Kearns and Inouye 1993). Samples were qualitatively scanned to note the major and minor pollen constituents. Floral sources were considered major constituents if they made up greater than 25% of the pollen volume in the sample while sources that made up less than 25% were considered minor; however, both major and minor floral hosts were included in flower surveys.

Floral host surveys

To measure floral host abundance, observers walked in progressively larger circles from a central point and counted open flowers (or, in the case of Asteraceae, capitula with at least one open disk floret) until a total of 100 flowers of each taxon or a distance of 100 m (straight-line distance) from the centre was reached, whichever came first. The distance (r) to the 100th flower was then measured so that floral density could be calculated as $100/\pi r^2$ (Forrest and Chisholm 2017). If fewer than 100 flowers of a taxon were encountered within a 100 m radius, its floral density was considered to be 0.

Floral density per individual

Taraxacum officinale (Common Dandelion; Asteraceae) is a non-native, early-flowering species at our study sites, the pollen of which is occasionally found in brood cell pollen samples of *Osmia coloradensis*, *O. montana*, and *O. subaustralis* (Asteraceae specialists). This species was only included in flower surveys starting in 2016 (see Table S1. 2). To account for the inconsistent inclusion of *T. officinale* in floral surveys, we ran multivariate models for Question 2 twice for each aster specialist bee: once with *T. officinale* densities included in floral density values, and once with *T. officinale* excluded (for all years in which it was counted). Similarly, several floral hosts used by *H. fulgida* (*Allium brandegeei*, *Arctostaphylos uva-ursi*, *Geranium* spp., *Viola* spp., as well as *T. officinale*) were not consistently surveyed across years (see Table S1. 2). We therefore ran models first, with all the floral hosts of *H. fulgida* included regardless of whether they had been counted consistently, and secondly, with only consistently counted taxa. Results of GAMMs remained statistically and qualitatively identical (with minor differences in EDF values). Results reported in the main text (Table 1.1 & Table 1.2 in the main text) show results from models that include *T. officinale* and all hosts (including inconsistently counted taxa) for the aster specialists and for *H. fulgida* respectively. Specific differences in statistical values can be found in R scripts.

Linear and generalized linear mixed-effects models (LMMs & GLMMs)

We used the “lmer” and “glmer” functions for LMMs and GLMMs (GLMMs for Question 1b only) respectively in the R package “lme4” (Bates et al., 2015). For LMMs, significance of fixed factors was evaluated with Satterthwaite-approximated degrees of freedom using the “lmerTest” package (Kuznetsova et al. 2017). To assess goodness-of-fit, we calculated marginal R^2 values for all model predictors using the “rsquared.GLMM” function in the R package MuMIn (Bartoń 2020). For all LMMs for Question 2, we calculated Variance Inflation Factors (VIFs) using the “corvif” function described by (Zuur et al. 2009). VIFs were all moderate (maximum = 3.2), suggesting that multicollinearity was not severe (Zuur et al. 2009).

Table S1. 1. Study site information.

Sites used in the study, showing years in which each site was used.

Site name	Latitude (°N)	Longitude (°W)	Elevation (m)	Years surveyed
Brush Creek	38°51'39.8"	106°55'10.2"	2729	2013–2018
401 Trail	38°57'41.7"	106°59'5.6"	2970	2013–2018
Kebler Clearing	38°51'30.9"	107°3'37.7"	2958	2014–2018
Kebler Pass	38°51'5.0"	107°6'0.0"	3034	2014–2018
Mt. Crested Butte	38°53'21.1"	106°57'44.3"	2889	2013–2015
Rosy Point	38°55'57.6"	106°58'12.6"	2900	2013–2018
Virginia Basin*	38°58'55.8"	106°58'20.0"	3440	2013–2018

* Visits to Virginia Basin were made less frequently compared to the other sites as its high-elevation location made this site less easily accessible

Table S1. 2. List of plant taxa surveyed.

Plant taxa for which floral density was measured in each year of the study (2013–2018; see Supplementary methods: Floral host surveys for details on how floral density was estimated). A dash indicates that a taxon was not counted in a given year. Some taxa that were counted separately in the early years of the study were combined in later years (e.g., Boraginaceae spp., Rosaceae spp.).

Family	2013	2014	2015	2016	2017	2018
Amaryllidaceae	—	—	—	—	—	<i>Allium brandegeei</i>
Asteraceae	<i>Erigeron & Aster</i> spp.	<i>Erigeron & Aster</i> spp.	<i>Erigeron & Aster</i> spp.	<i>Erigeron & Aster</i> spp.	<i>Erigeron & Aster</i> spp.	<i>Erigeron & Aster</i> spp.
	<i>Helianthella quinquenervis</i>	<i>Helianthella quinquenervis</i>	<i>Helianthella quinquenervis</i>	<i>Helianthella quinquenervis</i>	<i>Helianthella quinquenervis</i>	<i>Helianthella quinquenervis</i>
	<i>Heliomeris multiflora</i>	<i>Heliomeris multiflora</i>	<i>Heliomeris multiflora</i>	<i>Heliomeris multiflora</i>	<i>Heliomeris multiflora</i>	<i>Heliomeris multiflora</i>
	<i>Heterotheca villosa</i>	<i>Heterotheca villosa</i>	<i>Heterotheca villosa</i>	<i>Heterotheca villosa</i>	<i>Heterotheca villosa</i>	<i>Heterotheca villosa</i>
	<i>Hymenoxys hoopesii</i>	<i>Hymenoxys hoopesii</i>	<i>Hymenoxys hoopesii</i>	<i>Hymenoxys hoopesii</i>	<i>Hymenoxys hoopesii</i>	<i>Hymenoxys hoopesii</i>
	—	—	—	—	—	Other ligulate composites
	<i>Pyrrocoma crocea</i>	<i>Pyrrocoma crocea</i>	<i>Pyrrocoma crocea</i>	<i>Pyrrocoma crocea</i>	<i>Pyrrocoma crocea</i>	<i>Pyrrocoma crocea</i>
	<i>Senecio, Arnica, & Solidago</i> spp.	<i>Senecio, Arnica, & Solidago</i> spp.	<i>Senecio, Arnica, & Solidago</i> spp.	<i>Senecio, Arnica, & Solidago</i> spp.	<i>Senecio, Arnica, & Solidago</i> spp.	<i>Senecio, Arnica, & Solidago</i> spp.
	—	—	—	<i>Taraxacum officinale</i>	<i>Taraxacum officinale</i>	<i>Taraxacum officinale</i>
	<i>Wyethia amplexicaulis</i>	<i>Wyethia amplexicaulis</i>	<i>Wyethia amplexicaulis</i>	<i>Wyethia amplexicaulis</i>	<i>Wyethia amplexicaulis</i>	<i>Wyethia amplexicaulis</i>
Boraginaceae	—	—	<i>Hackelia floribunda</i>			
	<i>Mertensia ciliata</i>	<i>Mertensia ciliata</i>	<i>Mertensia ciliata</i>	Boraginaceae	Boraginaceae	Boraginaceae
	<i>Mertensia fusiformis & M. brevistyla</i>	<i>Mertensia fusiformis & M. brevistyla</i>	<i>Mertensia fusiformis & M. brevistyla</i>			
Ericaceae	—	—	<i>Arctostaphylos uva-ursi & Vaccinium</i> spp.	<i>Arctostaphylos uva-ursi & Vaccinium</i> spp.	<i>Arctostaphylos uva-ursi & Vaccinium</i> spp.	<i>Arctostaphylos uva-ursi & Vaccinium</i> spp.
Fabaceae	<i>Astragalus & Oxytropis</i> spp.	<i>Astragalus & Oxytropis</i> spp.	<i>Astragalus & Oxytropis</i> spp.	<i>Astragalus & Oxytropis</i> spp.	<i>Astragalus & Oxytropis</i> spp.	<i>Astragalus & Oxytropis</i> spp.
	<i>Lathyrus lanszwertii</i>	<i>Lathyrus lanszwertii</i>	<i>Lathyrus lanszwertii</i>	<i>Lathyrus lanszwertii</i>	<i>Lathyrus lanszwertii</i>	<i>Lathyrus lanszwertii</i>
	<i>Lupinus</i> spp.	<i>Lupinus</i> spp.	<i>Lupinus</i> spp.	<i>Lupinus</i> spp.	<i>Lupinus</i> spp.	<i>Lupinus</i> spp.
	<i>Vicia americana</i>	<i>Vicia americana</i>	<i>Vicia americana</i>	<i>Vicia americana</i>	<i>Vicia americana</i>	<i>Vicia americana</i>
Geraniaceae	<i>Geranium</i> spp.	<i>Geranium</i> spp.	<i>Geranium</i> spp.	—	—	—
Hydrophyllaceae	<i>Hydrophyllum capitatum</i>	<i>Hydrophyllum capitatum</i>	<i>Hydrophyllum capitatum</i>	Hydrophyllum spp.	Hydrophyllum spp.	Hydrophyllum spp.
	<i>Hydrophyllum fendleri</i>	<i>Hydrophyllum fendleri</i>	<i>Hydrophyllum fendleri</i>			

	<i>Phacelia</i> spp.	<i>Phacelia</i> spp.	<i>Phacelia</i> spp.	<i>Phacelia</i> spp.	<i>Phacelia</i> spp.	<i>Phacelia</i> spp.
Lamiaceae	<i>Agastache urticifolia</i>	<i>Agastache urticifolia</i>	<i>Agastache urticifolia</i>	<i>Agastache urticifolia</i>	<i>Agastache urticifolia</i>	<i>Agastache urticifolia</i>
Plantaginaceae	<i>Penstemon</i> spp.	<i>Penstemon</i> spp.	<i>Penstemon</i> spp.	<i>Penstemon</i> spp.	<i>Penstemon</i> spp.	<i>Penstemon</i> spp.
Polemoniaceae	<i>Polemonium</i> spp.	<i>Polemonium</i> spp.	<i>Polemonium</i> spp.	<i>Polemonium</i> spp.	<i>Polemonium</i> spp.	<i>Polemonium</i> spp.
Rosaceae	<i>Amelanchier alnifolia</i>	<i>Amelanchier alnifolia</i>	<i>Amelanchier alnifolia</i>			
	—	—	<i>Fragaria virginiana</i>	Rosaceae	Rosaceae	Rosaceae
	<i>Rosa woodsii</i>	<i>Rosa woodsii</i>	<i>Rosa woodsii</i>			
Violaceae	—	<i>Viola</i> spp.	<i>Viola</i> spp.	—	—	—

Table S1. 3. Summary of statistical models.

Summary of models and statistical approaches used to test study questions. GAMM = Generalized Additive Mixed-effects Model; LMM = Linear Mixed-effects Model; GLMM = Generalized Linear Mixed-effects Model. Models are written in the form $y \sim x + (1|R)$ where y , x , and R are the response, fixed predictor and random effect variables respectively. “Year” was normally coded as a random factor, except for analyses (1b) involving fewer than five years of data, in which case it was coded as a fixed categorical factor. Response variables were often square-root or fourth-root transformed to meet model assumptions (normality and homoscedasticity of residuals). Predictors were also sometimes log- or square root transformed to minimize the influence of a few extreme values.

#	Question	Model type	Model
1a	Consequences of nesting timing for individual reproduction	GAMM LMM	(Reproductive output) ^{0.5} ~ Nest initiation day + (1 Year) + (1 Site)
1b	Consequences of nesting timing for offspring success (<i>Hoplitis fulgida</i> only)	GLMM (binomial)	Cocoon success ~ Date laid + Year + (1 Site) + (1 Nest ID)
1b	Consequences of nesting timing for offspring success (<i>Hoplitis fulgida</i> only)	GLMM (binomial)	Proportion cocooned offspring ~ Nest initiation day + Year + (1 Site) Proportion emerged offspring ~ Nest initiation day + Year + (1 Site) <i>Total number of cells in each nest was included as a weight in both models</i>
1b	Consequences of nesting timing for offspring success	Pearson correlation	Proportion of cocooned offspring ~ Proportion of emerged offspring
2	Relationship between reproduction & environmental variables	GAMM LMM	(Reproductive output) ^{0.5} ~ Nest initiation day + (Floral density) ^{0.25} + Temperature + (1 Year) + (1 Site)
2	Relationship between reproduction & environmental variables	GAMM LMM	(Nesting rate) ^{0.5} ~ Day of the year + (Floral density) ^{0.25} + Temperature + (1 Year) + (1 Site) + (1 Nest identity)
*	Post hoc analysis: Relationship between reproduction & environmental variables, accounting for longevity (nesting duration)	GAMM LMM	(Reproductive output) ^{0.5} ~ Nest initiation day + (Floral density) ^{0.25} + Temperature + (Nesting duration) ^{0.25} + (1 Year) + (1 Site)
*	Post hoc analysis: Relationship between nesting duration & temperature	GAMM LMM	(Nesting duration) ^{0.25} ~ Temperature + (1 Year) + (1 Site)
*	Post hoc analysis: Relationship between nesting duration & nest initiation day	GAMM LMM	(Nesting duration) ^{0.25} ~ Nest initiation day + (1 Year) + (1 Site)

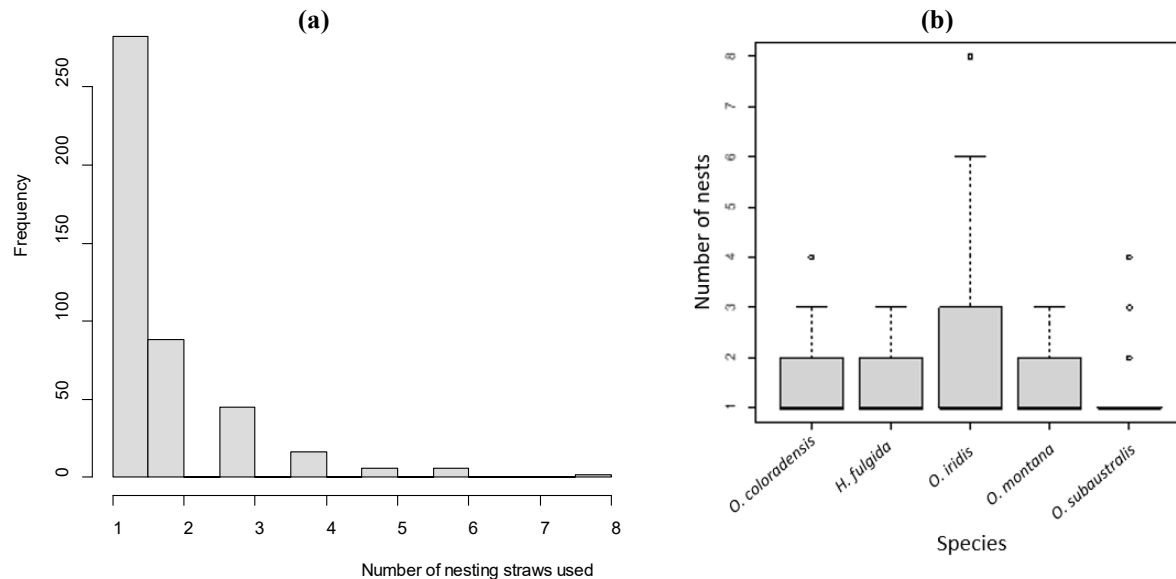


Figure S1. 3. Number of nests constructed per individual bee.

(a) Histogram of number of nesting straws used by individual bees. Approximately 63% of all observed individual bees used 1 nesting straw only (282/445) while the remaining individuals used more than 1 nesting straw. For these latter individuals, reproductive output was determined as the total number of brood cells produced summed across all straws (b) Number of nesting straws used by individual bees plotted by species. Box plots show median (dark line), third quartile (top of box), 1.5 times the interquartile range (whisker), and outliers (circles).

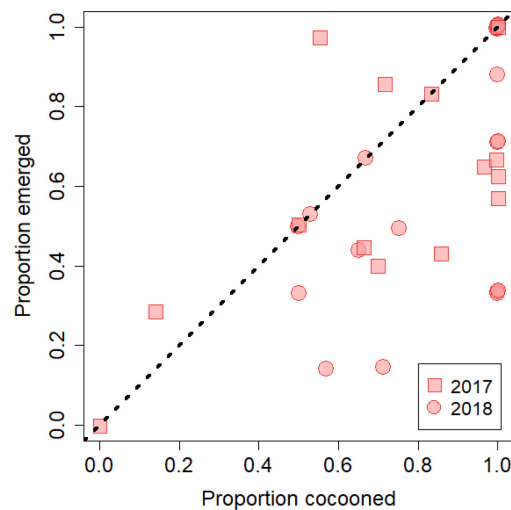


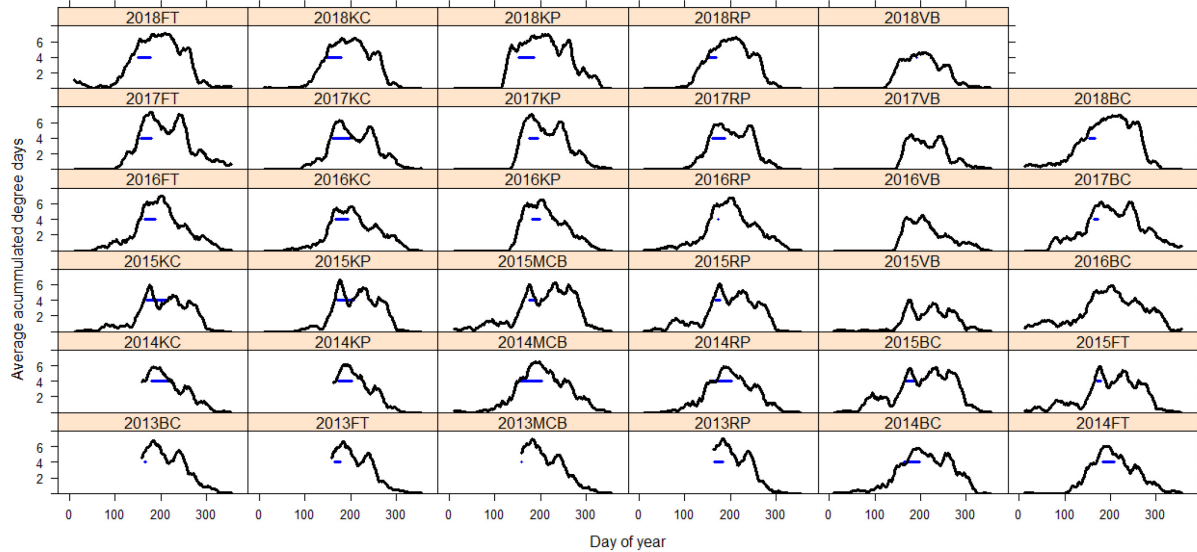
Figure S1. 4. Proportions of cocooned vs. emerged *H. fulgida* offspring.

Relationship between the proportions of *H. fulgida* offspring in each nest that successfully emerged and that successfully completed cocoons by the end of the summer for nests in 2017 and 2018. The dashed line represents a 1:1 ratio.

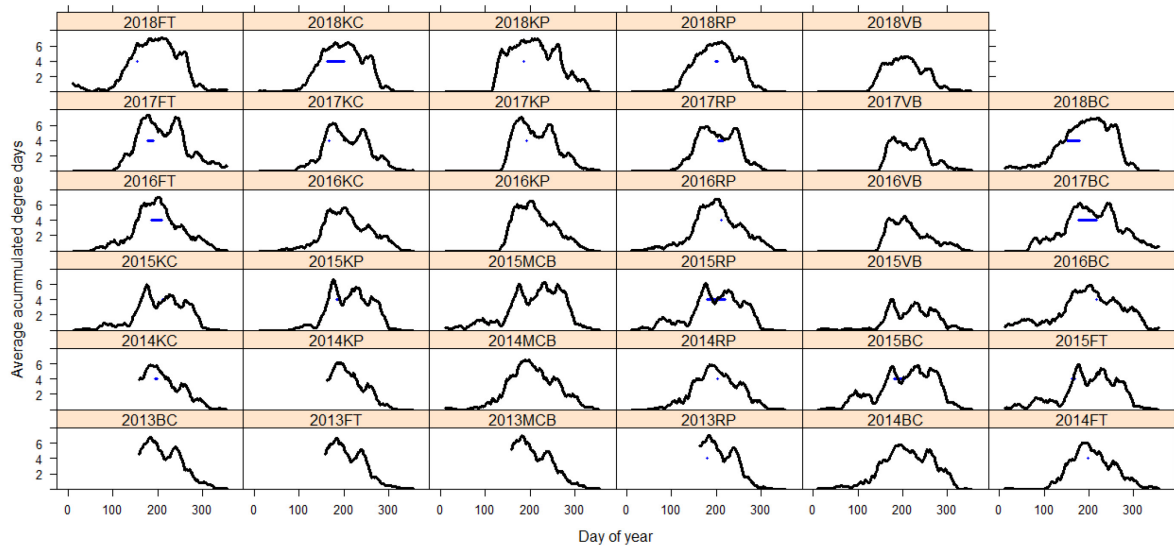
Figure S1. 5. Seasonal patterns of nesting and temperature (separated by bee species).

The following five figures supplement Figure 1.3d in the main text (there is one 6 x 6 panel figure for each species). Each panel shows the average accumulated daily degree-days above a threshold temperature of 10 °C (in black) over the course of the season at one unique site-year. The blue lines show the nesting period of the given species in the site-year (i.e., range between earliest and latest day on which a nest was initiated). The absence of a blue line indicates that the species was not recorded at the particular site-year.

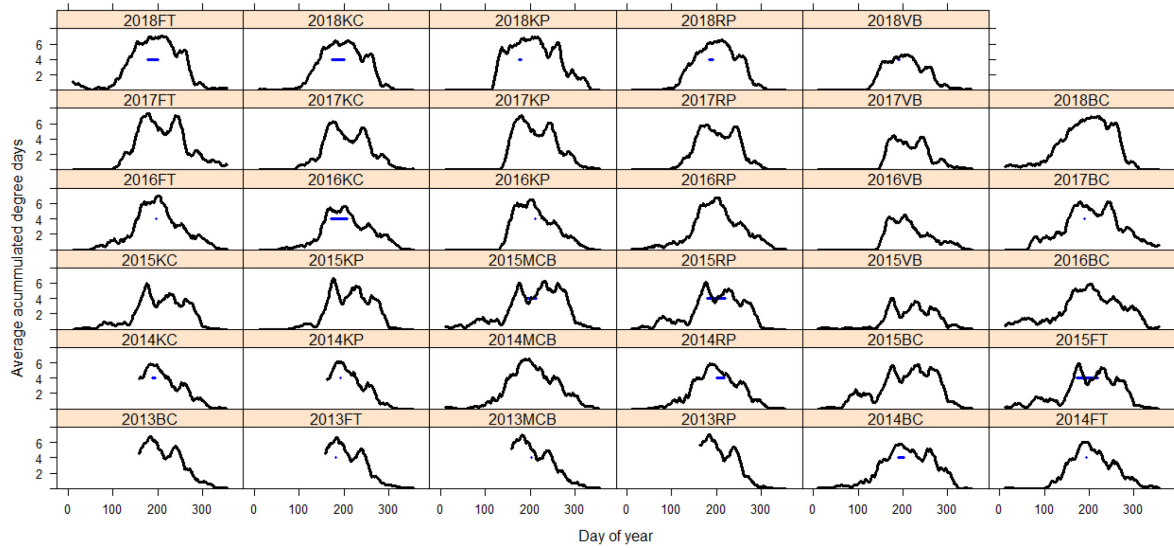
Osmia iridis



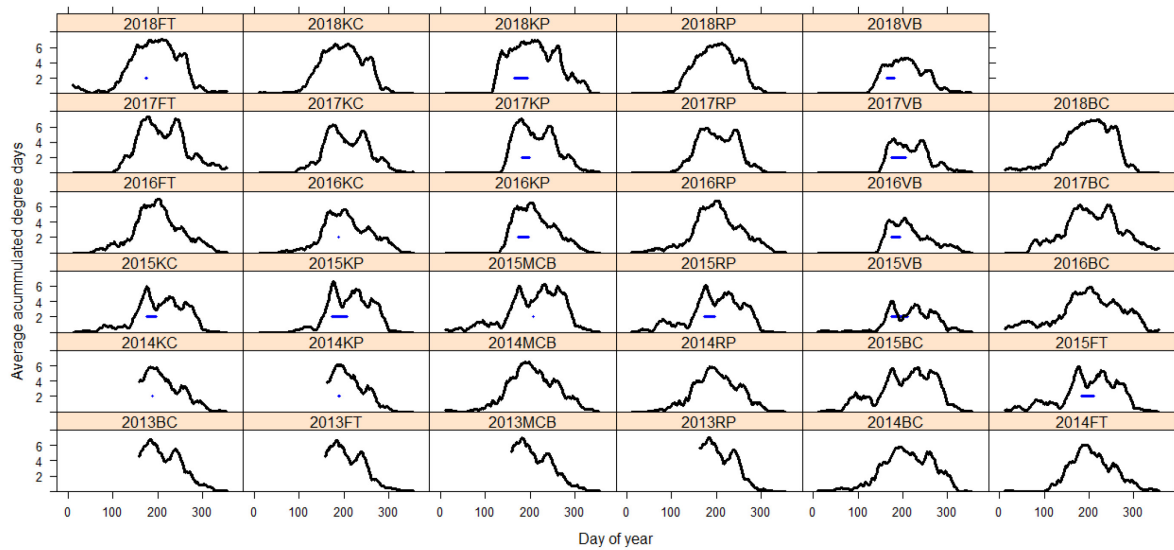
Osmia coloradensis



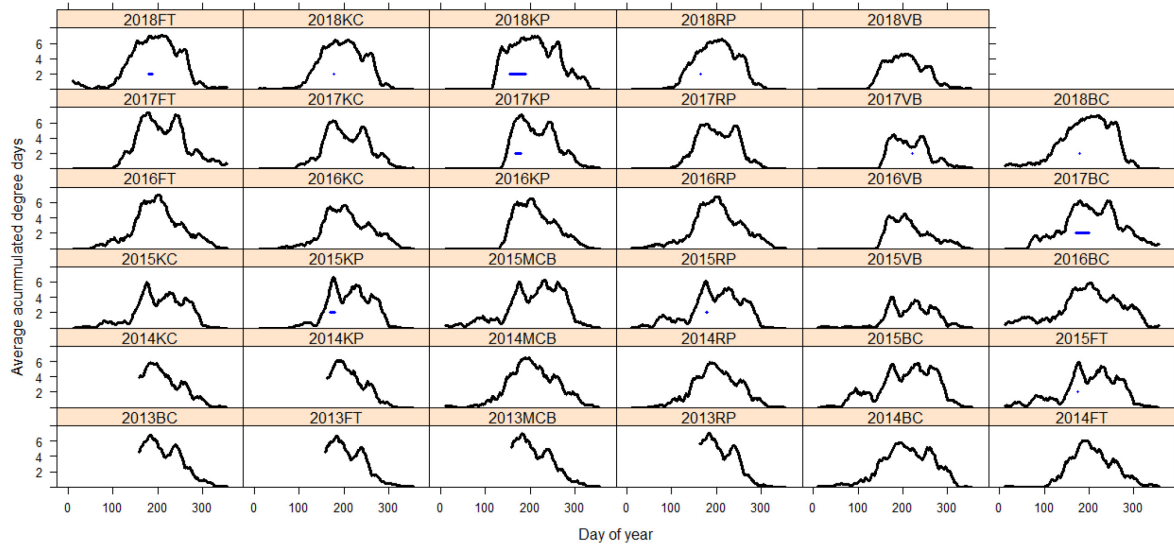
Osmia montana



Osmia subaustralis



Hoplitis fulgida



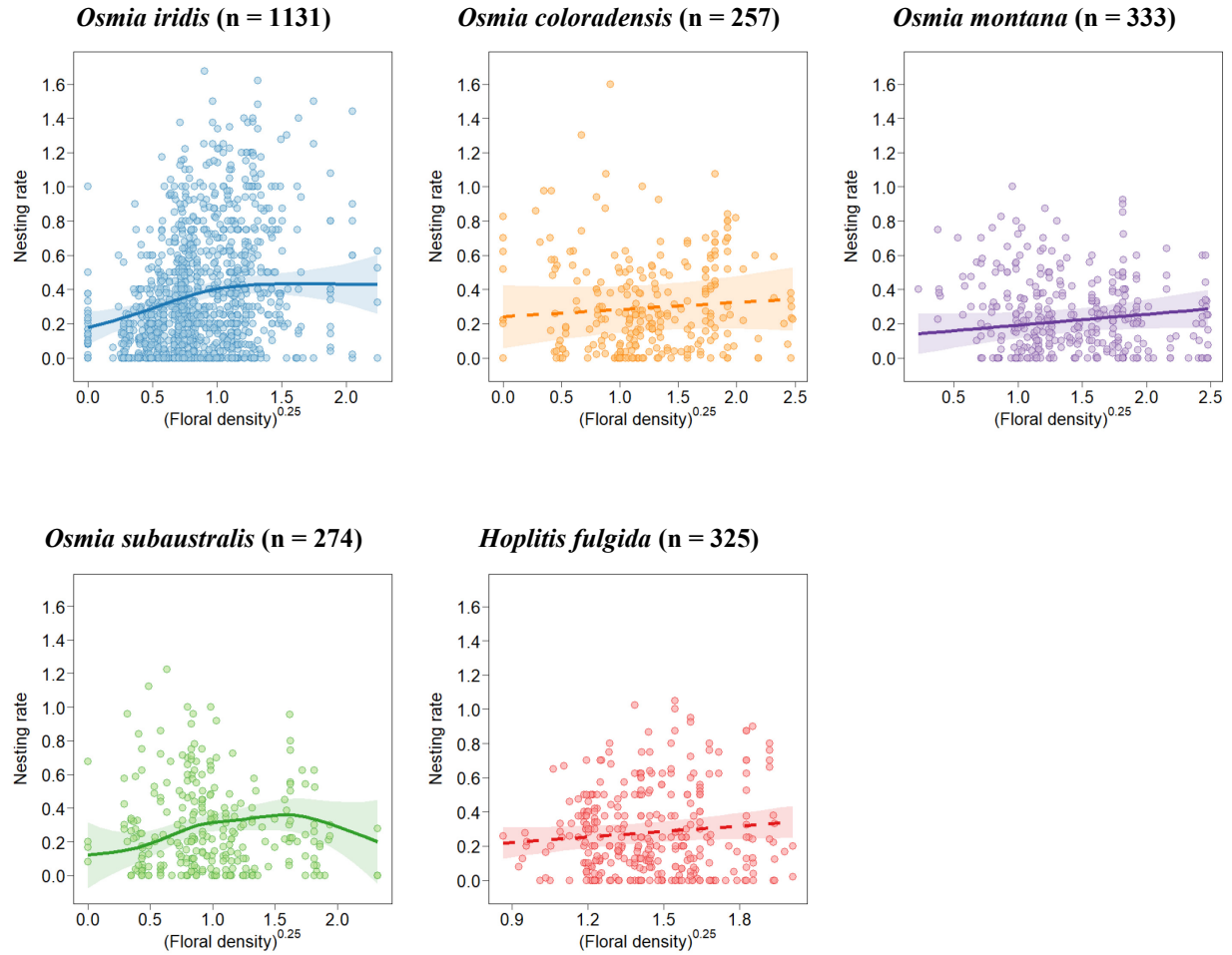


Figure S1. 6. Bee nesting rate vs. floral density (separated by bee species)

Bee nesting rate (number of brood cells constructed per day) as a function of floral density. Each datapoint in these figures represents one observation of a nesting bee (with multiple observations per bee). Data are from seven study sites across six years. Lines are GAMM fits from multivariate models described in the main text. Shading represents 95% confidence intervals of predictions. Lines are solid if the effect of the predictor is significant in multivariate models ($p < 0.05$) and dashed otherwise. Figure 1.4a in the main text shows identical information but without datapoints.

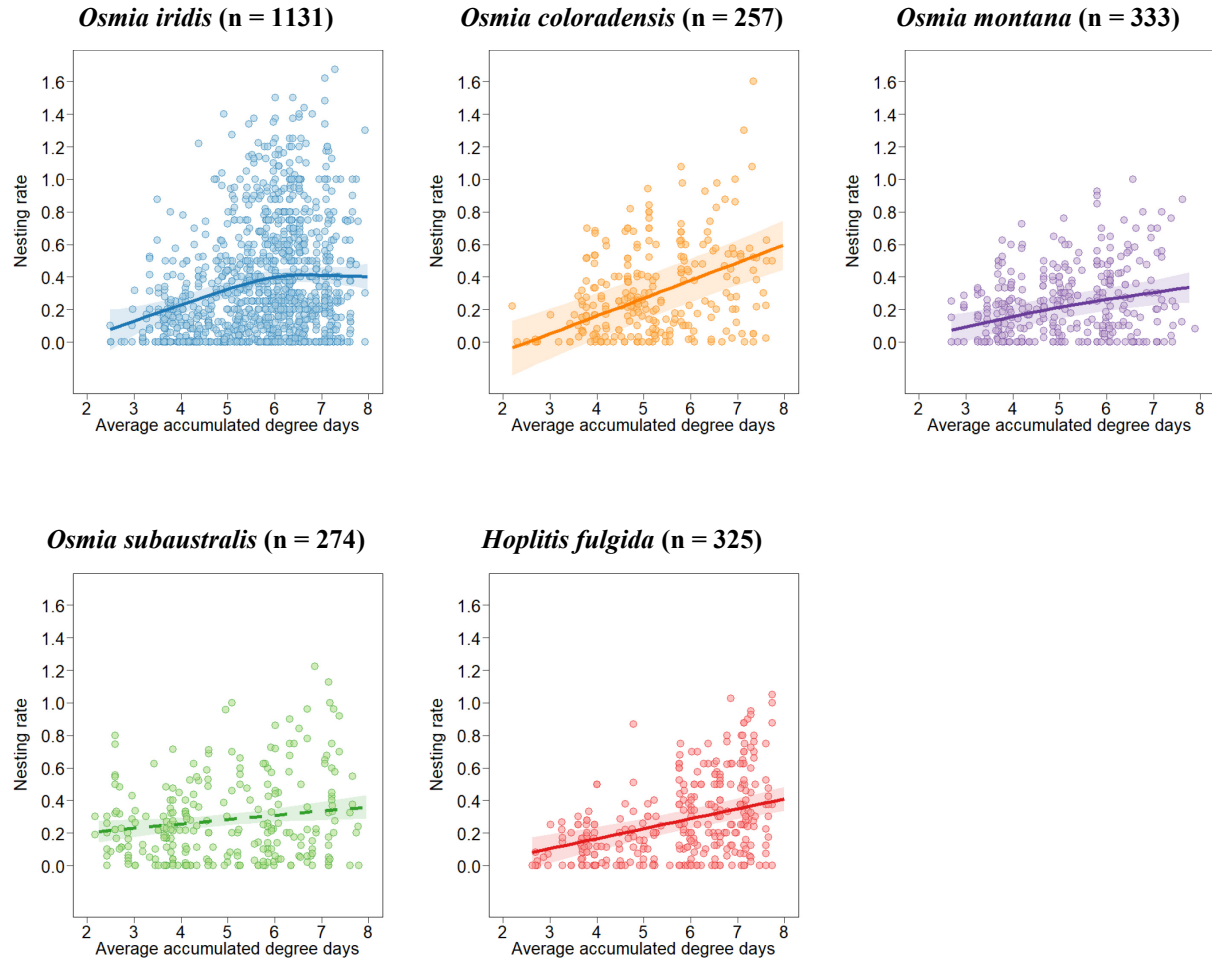


Figure S1. 7. Bee nesting rate vs. temperature (separated by bee species).

Bee nesting rate (number of brood cells constructed per day) as a function of average daily accumulated degree-days. Each datapoint in these figures represents one observation of a nesting bee (with multiple observations per bee). Data are from seven study sites across six years. Lines are GAMM fits from multivariate models (Table S1. 3). Shading represents 95% confidence intervals of predictions. Lines are solid if the effect of the predictor is significant in multivariate models ($p < 0.05$) and dashed otherwise. Figure 1.4b in the main text shows identical information but without datapoints.

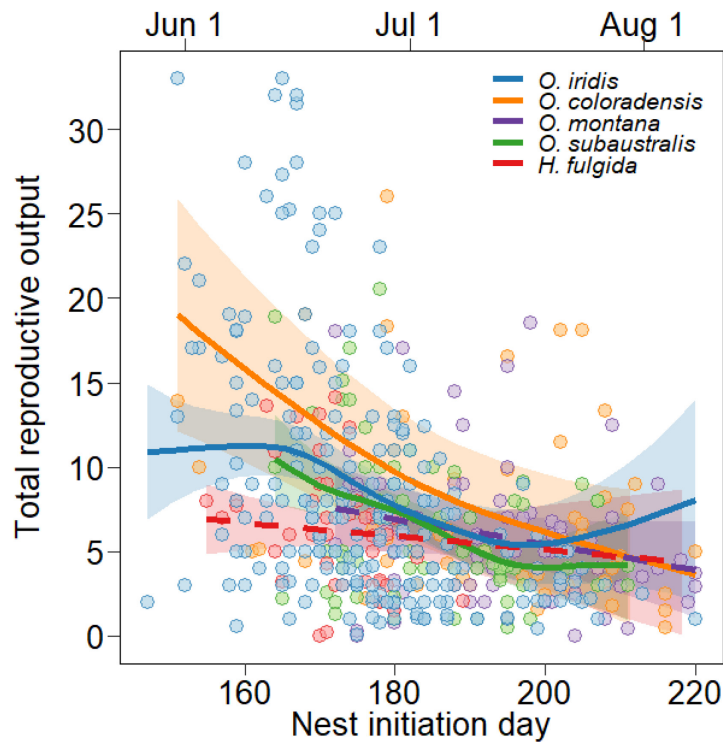


Figure S1. 8. Bee reproductive output vs. nest initiation day (post hoc) analysis.

Reproductive output vs. day of nest initiation after accounting for nesting duration (post hoc) for individual bees at seven study sites across six years. Lines are GAMM fits from post hoc multivariate models (Table 1.2). Shading represents 95% confidence intervals of predicted fits. Sample sizes (n): *Osmia iridis*: n = 208, *O. coloradensis*: n = 52, *O. montana*: n = 71, *O. subaustralis*: n = 66, *H. fulgida*: n = 48. in the main text shows the relationship between nest initiation day and reproductive output without having accounted for nesting duration. Datapoints in this figure are the same as in Figure 1.1, but fits in this figure account for nesting duration. Shading represents 95% confidence intervals of predictions. Sample sizes (n): *Osmia iridis*: n = 208, *O. coloradensis*: n = 52, *O. montana*: n = 71, *O. subaustralis*: n = 66, *H. fulgida*: n = 48.

Table S1. 4. Results of post hoc univariate generalized additive models.

General Additive Mixed-effects Model (GAMM) results and adjusted R^2 values for three univariate models. Year and site were included as random effects. Separate models were used for each species. edf = estimated degrees of freedom, where an edf = 1 indicates a linear relationship (i.e., no nonlinearities) and increasing values indicate increasingly complex nonlinear relationships. In some cases, R^2_{adj} values were low or zero possibly because insufficient sample sizes resulted in poor detection of the specific shapes of curves (i.e., the significant relationships suggest that directional relationships were detected, but the specific nonlinear pattern could not be identified). Because of this, even though models produced edf values of ~ 1 for these relationships, we note that the actual relationships in these cases may not actually be strictly linear.

Model	Species	edf	F	<i>p</i>	R^2_{adj}
Question 1a (reproductive output) ^{0.5} ~ nest initiation day	<i>O. iridis</i>	1.86	50.68	<0.001	0.228
	<i>O. coloradensis</i>	1	18.08	<0.001	0
	<i>O. montana</i>	1	9.72	0.003	0
	<i>O. subaustralis</i>	1	10.18	0.002	0.065
	<i>H. fulgida</i>	1	13.04	<0.001	0.185
Post hoc model (nesting duration) ^{0.25} ~ temperature	<i>O. iridis</i>	2.85	23.09	<0.001	0.27
	<i>O. coloradensis</i>	1	11.96	0.001	0.20
	<i>O. montana</i>	1	11.97	<0.001	0.12
	<i>O. subaustralis</i>	1	26.72	<0.001	0.28
	<i>H. fulgida</i> *	1.20	4.16	0.010	0.23
Post hoc model (nesting duration) ^{0.25} ~ nest initiation day	<i>O. iridis</i>	2.58	5.73	0.004	0.02
	<i>O. coloradensis</i>	1.20	5.67	0.013	0
	<i>O. montana</i>	1.86	5.52	0.019	0.08
	<i>O. subaustralis</i>	1	7.52	0.008	0
	<i>H. fulgida</i>	1	10.19	0.003	0.08

*an outlier with extremely high leverage was excluded for this model in *H. fulgida* as it produced an unrealistically non-linear GAM fit (documentation in R scripts). The effect of temperature on nesting duration remained significant with and without this outlier.

Table S1. 5. A priori results of linear models for bee reproductive output and nesting rate.

Linear mixed-effects model (LMM) results with bee reproductive output and nesting rate as a function of nest initiation day (day of year for rate), floral density, and average daily accumulated degree-days. Year and site were included as random effects. Bold indicates significant effects ($p < 0.05$).

Species	Response	Predictor	Estimate	SE	df	<i>t</i>	<i>p</i>
<i>O. iridis</i>	(Reproductive output) ^{0.5}	Nest initiation day	-0.060	0.008	167.1	-7.4	<0.001
		(Floral density) ^{0.25}	-0.243	0.322	192.1	-0.8	0.452
		Temperature	-0.139	0.074	195.5	-1.9	0.062
	(Nesting rate) ^{0.5}	Day of the year	-0.007	0	540.0	-7.0	<0.001
		(Floral density) ^{0.25}	0.130	0.030	756.8	4.4	<0.001
		Temperature	0.056	0.008	1014	7.3	<0.001
<i>O. coloradensis</i>	(Reproductive output) ^{0.5}	Nest initiation day	-0.060	0.009	44.5	-6.8	<0.001
		(Floral density) ^{0.25}	1.557	0.335	46.3	4.7	<0.001
		Temperature	-0.058	0.128	46.6	-0.5	0.654
	(Nesting rate) ^{0.5}	Day of the year	-0.004	0.002	207.5	-2.1	0.040
		(Floral density) ^{0.25}	0.077	0.051	93.9	1.5	0.138
		Temperature	0.106	0.015	247.6	7.1	<0.001
<i>O. montana</i>	(Reproductive output) ^{0.5}	Nest initiation day	-0.025	0.010	63.3	-2.6	0.011
		(Floral density) ^{0.25}	0.077	0.330	48.6	0.2	0.816
		Temperature	-0.292	0.114	53.8	-2.6	0.013
	(Nesting rate) ^{0.5}	Day of the year	-0.007	0.002	292.9	-4.4	<0.001
		(Floral density) ^{0.25}	0.108	0.049	192.4	2.2	0.030
		Temperature	0.050	0.013	307.6	3.9	<0.001
<i>O. subaustralis</i>	(Reproductive output) ^{0.5}	Nest initiation day	-0.077	0.009	57.6	-8.1	<0.001
		(Floral density) ^{0.25}	2.186	0.296	61.5	7.4	<0.001
		Temperature	0.035	0.064	61.9	0.5	0.588
	(Nesting rate) ^{0.5}	Day of the year	-0.002	0.002	29.5	-1.1	0.300
		(Floral density) ^{0.25}	0.048	0.066	54.5	0.7	0.477
		Temperature	0.040	0.013	78.4	3.0	0.004
<i>H. fulgida</i>	(Reproductive output) ^{0.5}	Nest initiation day	-0.033	0.011	44.0	-2.9	0.006
		(Floral density) ^{0.25}	1.031	0.623	44.0	1.7	0.105
		Temperature	-0.069	0.129	44.0	-0.5	0.597
	(Nesting rate) ^{0.5}	Day of the year	-0.006	0.001	120.9	-4.6	<0.001
		(Floral density) ^{0.25}	0.100	0.063	273.5	1.6	0.116
		Temperature	0.061	0.012	313.3	4.9	<0.001

Table S1. 6. Post hoc results of linear models for bee reproductive output.

Post hoc linear mixed-effects model (LMM) results of bee reproductive output as a function of nest initiation day, floral density, average daily accumulated degree-days, and nesting duration. Year and site included as random effects. Bold indicates significant results ($p < 0.05$). Marginal R^2 values (R^2_m) were determined using univariate LMMs.

Species	Predictor	Estimate	SE	df	<i>t</i>	<i>p</i>	R^2_m
<i>O. iridis</i>	Nest initiation day	-0.028	0.006	164.1	-4.8	<0.001	0.313
	(Floral density) ^{0.25}	0.582	0.223	181.2	2.6	0.010	0.104
	Temperature	0.317	0.058	200.4	5.5	<0.001	<0.001
	(Nesting duration) ^{0.25}	2.590	0.166	198.8	15.6	<0.001	0.388
<i>O. coloradensis</i>	Nest initiation day	-0.041	0.012	42.6	-3.5	0.001	0.239
	(Floral density) ^{0.25}	1.102	0.386	44.6	2.9	0.007	0.006
	Temperature	0.114	0.148	46.5	0.7	0.444	<0.001
	(Nesting duration) ^{0.25}	1.007	0.467	46.2	2.2	0.036	0.321
<i>O. montana</i>	Nest initiation day	-0.008	0.010	39.7	-0.8	0.436	0.123
	(Floral density) ^{0.25}	-0.175	0.336	21.0	-0.5	0.609	0.004
	Temperature	-0.057	0.127	14.2	-0.4	0.662	0.080
	(Nesting duration) ^{0.25}	1.403	0.354	63.5	4.0	<0.001	0.290
<i>O. subaustralis</i>	Nest initiation day	-0.022	0.007	60.7	-2.9	0.005	0.112
	(Floral density) ^{0.25}	0.621	0.253	60.8	2.5	0.017	0.085
	Temperature	0.144	0.057	40.5	2.5	0.016	0.072
	(Nesting duration) ^{0.25}	2.264	0.280	56.6	8.1	<0.001	0.683
<i>H. fulgida</i>	Nest initiation day	-0.011	0.012	17.0	-0.8	0.409	0.217
	(Floral density) ^{0.25}	1.226	0.579	8.3	2.1	0.066	0.117
	Temperature	0.156	0.127	43.0	1.2	0.227	0.012
	(Nesting duration) ^{0.25}	1.842	0.483	42.9	3.8	<0.001	0.312

Table S1. 7. Results of post hoc univariate linear models.

Linear mixed-effects models (LMM) results and marginal R^2 (R^2_m) values for three univariate models. Year and site were included as random effects. Separate models were used for each species.

Model	Species	Estimate	SE	df	<i>t</i>	<i>p</i>	R^2_m
Question 1a reproductive output) ^{0.5} ~ nest initiation day	<i>O. iridis</i>	-0.053	0.006	192.2	-9.0	<0.001	
	<i>O. coloradensis</i>	-0.034	0.007	49.9	-4.5	<0.001	See
	<i>O. montana</i>	-0.025	0.009	66.0	-3.0	0.004	Table
	<i>O. subaustralis</i>	-0.025	0.009	51.4	-2.8	0.007	S1. 6
	<i>H. fulgida</i>	-0.037	0.010	45.6	-3.6	<0.001	
Post hoc model (nesting duration) ^{0.25} ~ Temperature	<i>O. iridis</i>	-0.154	0.020	123.6	-7.6	<0.001	0.226
	<i>O. coloradensis</i>	-0.131	0.036	50	-3.7	<0.001	0.210
	<i>O. montana</i>	-0.124	0.036	11.1	-3.5	0.005	0.172
	<i>O. subaustralis</i>	-0.116	0.022	64	-5.2	<0.001	0.291
	<i>H. fulgida</i>	-0.055	0.037	45.0	-1.5	0.183	0.047
Post hoc model (nesting duration) ^{0.25} ~ nest initiation day	<i>O. iridis</i>	-0.003	0.002	61.9	-1.6	0.120	0.013
	<i>O. coloradensis</i>	-0.008	0.002	48.0	-3.5	0.001	0.170
	<i>O. montana</i>	-0.008	0.003	57.5	-2.7	0.008	0.104
	<i>O. subaustralis</i>	-0.007	0.003	61.4	-2.5	0.016	0.072
	<i>H. fulgida</i>	-0.010	0.003	40.8	-3.3	0.002	0.185

Table S1. 8. Pairwise concurrency indices for bee reproductive output models.

Estimated pairwise concurrency indices for multivariate models testing the effects of nest initiation day, floral density, temperature, and nesting duration on bee reproductive output. Values are bounded between 0 and 1 indicating no and full concurrency respectively. Details in main text and in (Wood 2020).

Osmia iridis:

	Nest initiation day	Floral density	Temperature	Nesting duration
Nest initiation day		0.45	0.14	0.04
Floral density	0.4		0.12	0.05
Temperature	0.13	0.08		0.26
Nesting duration	0.05	0.03	0.23	

Osmia coloradensis:

	Nest initiation day	Floral density	Temperature	Nesting duration
Nest initiation day		0.52	0.25	0.26
Floral density	0.58		0.23	0.19
Temperature	0.38	0.33		0.39
Nesting duration	0.18	0.08	0.27	

Osmia montana:

	Nest initiation day	Floral density	Temperature	Nesting duration
Nest initiation day		0.51	0.3	0.18
Floral density	0.45		0.41	0.24
Temperature	0.24	0.41		0.19
Nesting duration	0.27	0.08	0.16	

Osmia subaustralis:

	Nest initiation day	Floral density	Temperature	Nesting duration
Nest initiation day		0.44	0.19	0.13
Floral density	0.5		0.32	0.27
Temperature	0.13	0.29		0.28
Nesting duration	0.3	0.25	0.34	

Hoplitis fulgida:

	Nest initiation day	Floral density	Temperature	Nesting duration
Nest initiation day		0.26	0.56	0.29
Floral density	0.14		0.13	0.11
Temperature	0.55	0.2		0.38
Nesting duration	0.39	0.17	0.44	

Table S1. 9. Pairwise concavity indices for bee nesting rate models.

Estimated pairwise concavity indices for multivariate models testing the effects of day of year, floral density and temperature on bee nesting rate. Values are bounded between 0 and 1 indicating no and full concavity respectively. Details in main text and in (Wood 2020).

Osmia iridis

	Day of year	Floral density	Temperature
Day of year		0.29	0.19
Floral density	0.28		0.06
Temperature	0.11	0.05	

Osmia coloradensis

	Day of year	Floral density	Temperature
Day of year		0.55	0.19
Floral density	0.58		0.18
Temperature	0.28	0.16	

Osmia montana

	Day of year	Floral density	Temperature
Day of year		0.53	0.3
Floral density	0.55		0.24
Temperature	0.34	0.22	

Osmia subaustralis

	Day of year	Floral density	Temperature
Day of year		0.58	0.24
Floral density	0.6		0.2
Temperature	0.23	0.17	

Hoplitis fulgida

	Day of year	Floral density	Temperature
Day of year		0.2	0.39
Floral density	0.11		0.07
Temperature	0.47	0.18	

Appendix B - Chapter 2 Supplementary information

Table S2. 1. Site information.

Site names, site abbreviations, years in which they were monitored, elevation, and distance from the RMBL (study location for long-term dataset used in analysis of floral resource abundance). VB was visited weekly as its high elevation meant that bee nesting progressed more slowly (hence requiring less frequent monitoring).

	2013	2014	2015	2016	2017	2018	2019	2021	2022	Elevation (m)	Frequency of site visits	Distance from RMBL (km)
Brush Creek (BC)	x	x	x	x	x	x	x	x	x	2729		12
401 Trail (FT)	x	x	x	x	x	x	x	x	x	2970		1.6
Kebler Clearing (KC)		x	x	x	x	x	x	x	x	2958	Every 3–5 days	12.3
Kebler Pass (KP)		x	x	x	x	x	x	x	x	3034		15
Mount Crested Butte (MC)	x	x	x							2889		7.5
Rosy Point (RP)	x	x	x	x	x	x	x	x	x	2900		3.2
Virginia Basin (VB)	x	x	x	x	x	x	x	x	x	3400	Weekly	2.5
Rocky Mountain Biological Laboratory (RMBL)	x	x	x	x	x	x	x	x	x	2900	Every 2–3 days	NA

Floral groups

Table S2. 2. Floral hosts of focal bee species.

Floral groups for each bee species and approximate number of floral host species in each group; the number and identity of species vary among sites. Floral host usage was determined by examining pollen samples taken from pollen-nectar provisions in nests under a microscope. Species numbers are approximate and given as ranges for the asteraceae and generalist floral groups because counts of congeneric plant species were combined during surveys and the exact number of distinct host species at some sites is unclear (Forrest 2024). Note that numbers do not reflect the number of host species available to bees at any given time as species vary in flowering phenology and not all species occur at each site. Floral host usage was determined by examining pollen samples taken from pollen-nectar provisions in nests under a microscope.

Bee species	Floral group	Number of floral host species used
<i>O. coloradensis</i>		
<i>O. montana</i>	Asteraceae	~10–15
<i>O. subaustralis</i>		
<i>Osmia iridis</i>	Fabeae (tribe)	2
<i>O. tristella</i>	Generalist hosts	~30–40

Additional details on temperature data

HOBO data were downloaded annually and batteries exchanged as needed to ensure that they continued to log throughout the course of the study, even through the winter months when we were not present.

Some of the climate metrics we used in analysis covered months prior to initial site (and HOBO) establishment in the spring of 2013 and 2014. For example, water-year drought severity (September of the previous year to August of the current year) for 2013 requires temperature data from September–December 2012, and January–April 2013. In these cases, we accessed daily temperature data using the parameter-elevation regressions on independent slopes model (PRISM). We then imputed the missing temperatures using the relationship between PRISM temperatures and available HOBO data from the specific site for which data were missing. These imputed temperatures contributed to metrics for only 7 out of 55 site-years analysed.

Supplemental Results

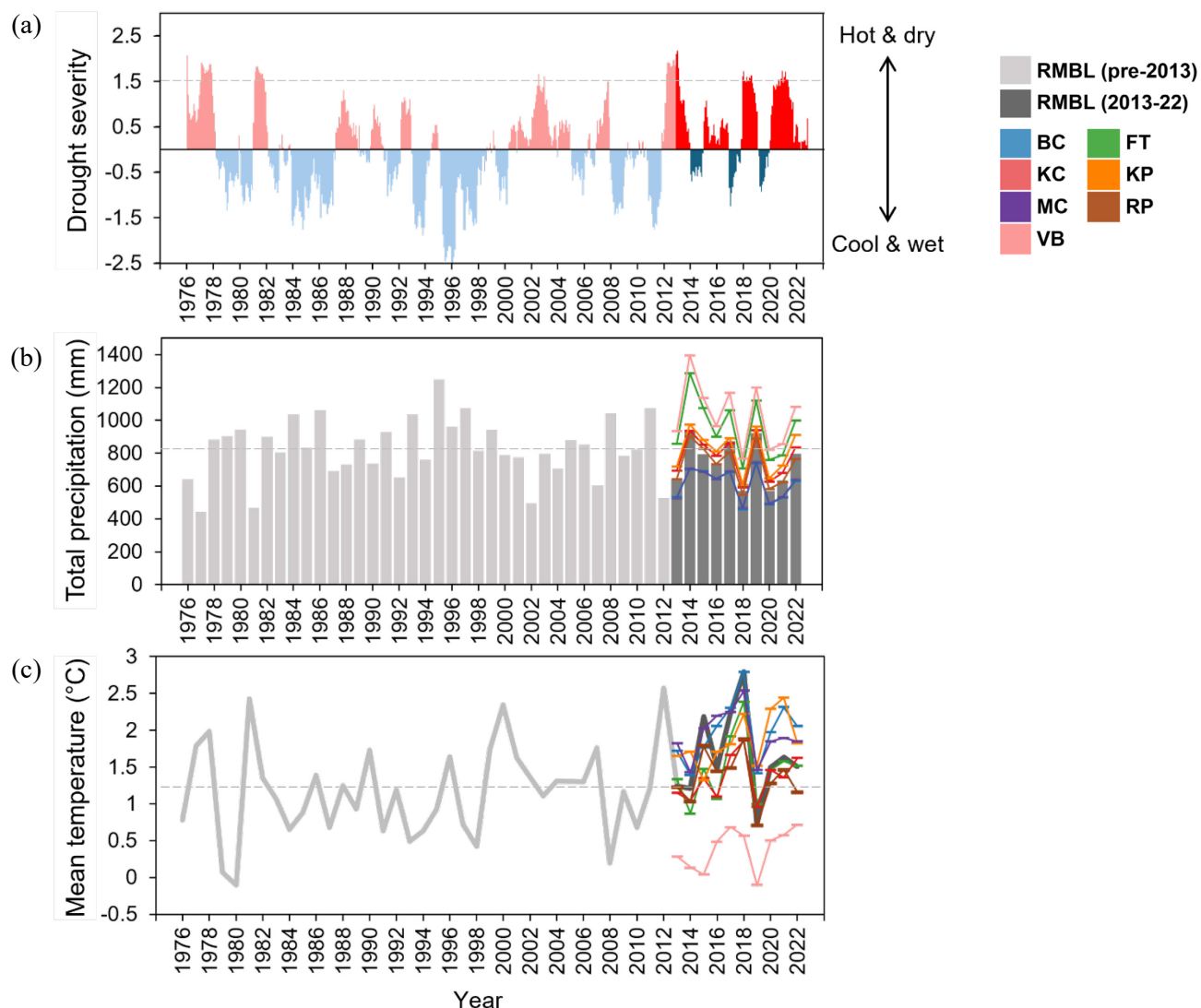


Figure S2. 1. Yearly climate data for the RMBL from 1976–2022.

(a) Drought severity ($-1 \times 12\text{-month Standardized Precipitation-evapotranspiration index}$), (b) Total water-year precipitation and (c) Water-year mean temperature from 1976–2022. Data in (a) are for the Rocky Mountain Biological Laboratory (RMBL; long-term site) only. Data in (b) and (c) are for both the seven study sites and the RMBL. Site abbreviations are in Table S2. 1. Climate data captured prior to bee monitoring (RMBL data) are semitransparent (a), or in light grey (b, c). In (c), temperatures at the seven study sites are scaled to the range of RMBL temperatures for visualization and do not reflect temperatures measured in the field. Sensor placement differed between studies resulting in different temperature ranges; this panel serves to contextualize temperature conditions from 2013–2022 relative to previous decades (e.g., number and frequency of historical “extremes”) and to visualize the extent to which conditions at the seven study sites reflected these temporal patterns. For (a), large positive values indicate severe drought; large negative values indicated cooler and wetter conditions. Drought severity for all sites are in Figure S2. 2. Horizontal dashed lines represent median values for the baseline period 1976–2012.

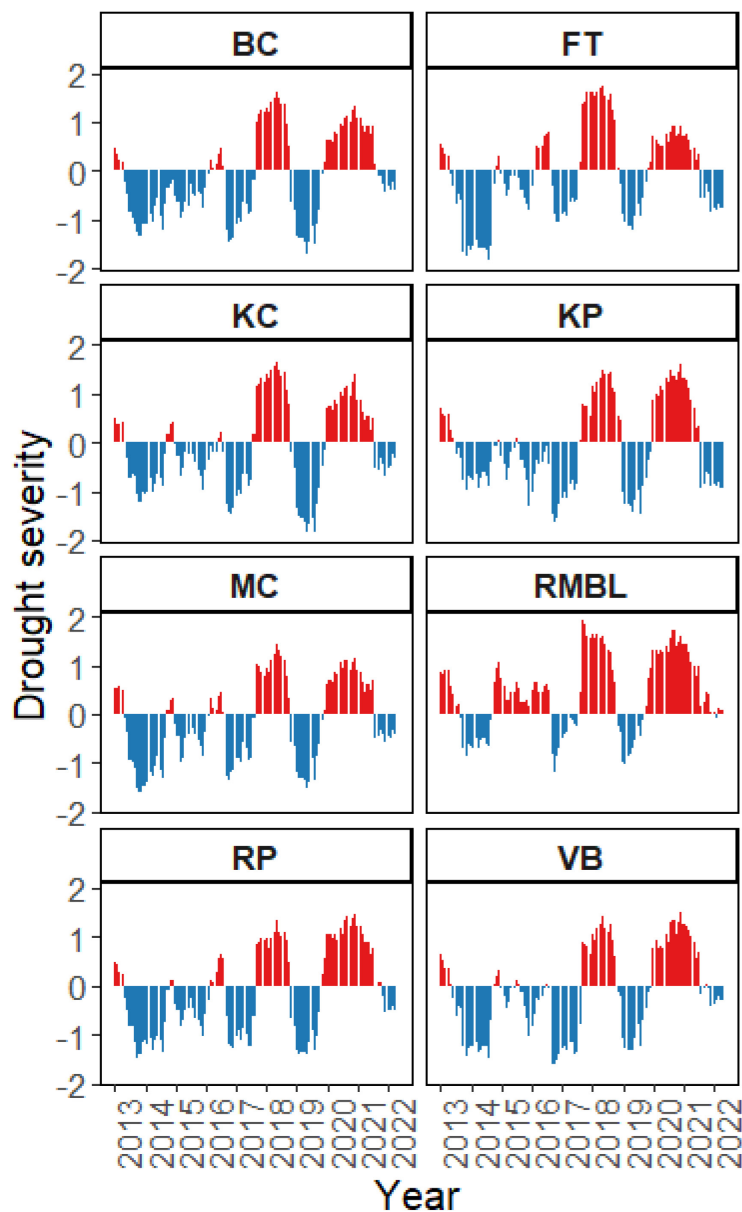


Figure S2. 2. Drought severity from 2013–2022.

Drought severity ($-1 \times 12\text{-month Standardized Precipitation-evapotranspiration index}$) for each of the seven study sites and the RMBL from May 2013 to August 2022. See Table S2. 1 for site abbreviations. Large positive values (red) indicate hotter and drier conditions, large negative values (blue) indicate cooler and wetter conditions.

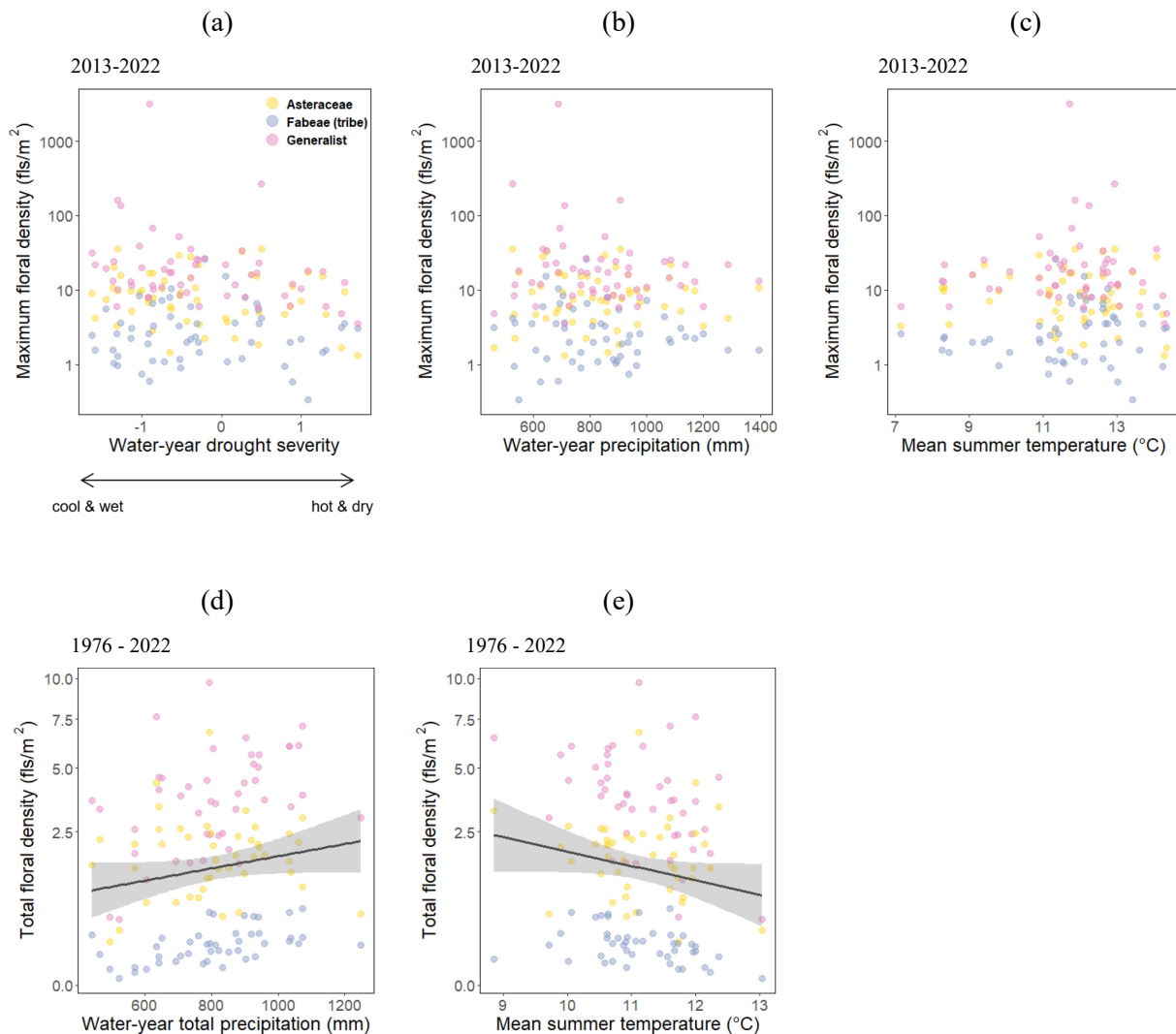


Figure S2. 3. Floral density vs. climate variables (7 sites and the RMBL).

Relationships between floral density and climate variables at the seven study sites (a-c; 2013–2022) and at the RMBL (b-d; 1976–2022) for the three floral groups as a function of (a) water-year drought severity (-1×12 -month Standardized Precipitation-Evapotranspiration Index), (b, d) total water-year precipitation, and (c, e) mean summer temperature. For (a–c), all three relationships were non-significant as fixed independent effects in the multivariate model reported in the text, but the interactive effects of temperature and precipitation were significant. In (a–c), each datapoint represents the maximum floral density observed for a given floral group in a given site and year. $n=55$ site-years for each floral group. In (d & e), each datapoint represents the total floral density in a given year. $n=45$ years per floral group. The y-axis was log₁₀- and square-root scaled in (a–c) and (d, e) respectively to better visualize all datapoints including some extreme values. Marginal R^2 values for predictors are in Table S2. 6. Figure 2.2 in the main text shows the relationship between drought severity and total floral density at the RMBL.

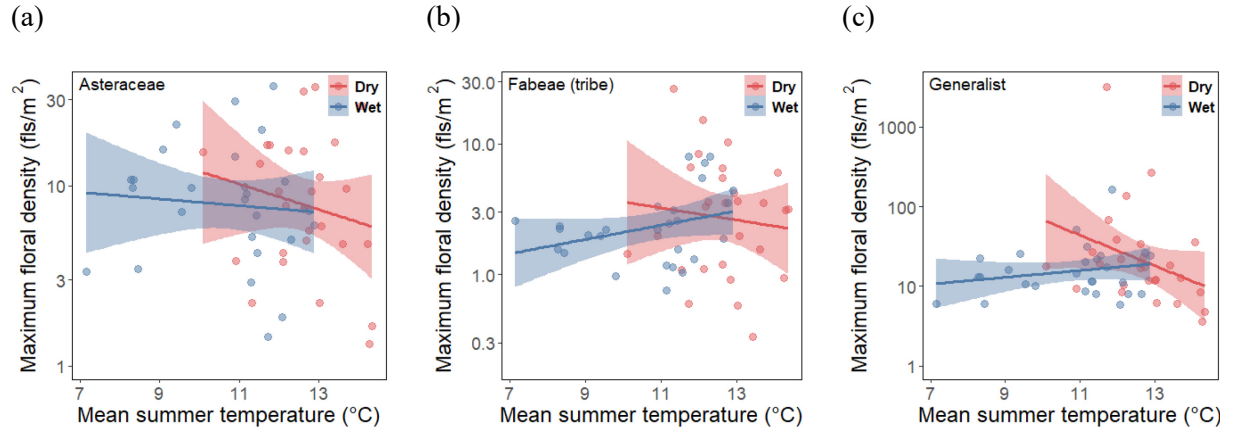


Figure S2. 4. Interactive effects of temperature and precipitation on floral density (7 sites).

Floral density at seven study sites (2013–2022) as a function of mean summer temperature for (a) Asteraceae (b) tribe Fabeae, and (c) generalist floral hosts. Data are divided into two equal precipitation categories based on total water-year precipitation for visualization purposes. “Dry” and “Wet” correspond to water-year precipitation totals less than and greater than the median water-year precipitation, respectively (827 mm). Red lines have more negative slopes than the blue lines. Each datapoint represents maximum floral density for a given site and year; $n=55$ site-years for each floral group. Bands indicate 95% confidence intervals for the slope of simple univariate linear models. Note $\log_{10}$ - scaling of y-axes. Marginal R^2 values are in Table S2. 6.

Table S2. 3. Mean number of brood cells per bee.

Mean number of brood cells produced per individual for the five *Osmia* species in each year of the study. Numbers of individuals observed are in parentheses. Total brood cell production was recorded as a decimal value in the field as we included partially complete brood cells but rounded to the nearest integer for statistical models.

Year	<i>O. iridis</i>	<i>O. coloradensis</i>	<i>O. montana</i>	<i>O. subaustralis</i>	<i>O. tristella</i>	All species
2013	13.35 (13)	26 (1)	10 (2)	0	10.94 (8)	12.79 (24)
2014	8.06 (53)	6.14 (5)	5.62 (15)	4.34 (5)	8.17 (3)	7.26 (81)
2015	6.73 (44)	8.83 (21)	6.7 (32)	7.43 (26)	8.75 (13)	7.38 (136)
2016	8.58 (20)	3.3 (5)	4.19 (9)	4.84 (13)	5.7 (3)	6.11 (50)
2017	9.14 (40)	5.25 (13)	3.5 (2)	4.29 (9)	6.05 (4)	7.41 (68)
2018	6.64 (52)	5.04 (11)	4.63 (17)	6.43 (17)	4.66 (5)	6 (102)
2019	8.64 (48)	16.5 (11)	5.9 (1)	11 (7)	9.5 (2)	10.12 (69)
2021	4.87 (31)	5.93 (13)	6.1 (15)	5.52 (17)	1.07 (3)	5.27 (79)
2022	4.82 (61)	6.07 (6)	8.33 (22)	6.4 (21)	7 (4)	5.93 (114)
All years	7.29 (362)	7.88 (86)	6.29 (115)	6.36 (115)	7.57 (45)	7.07 (723)

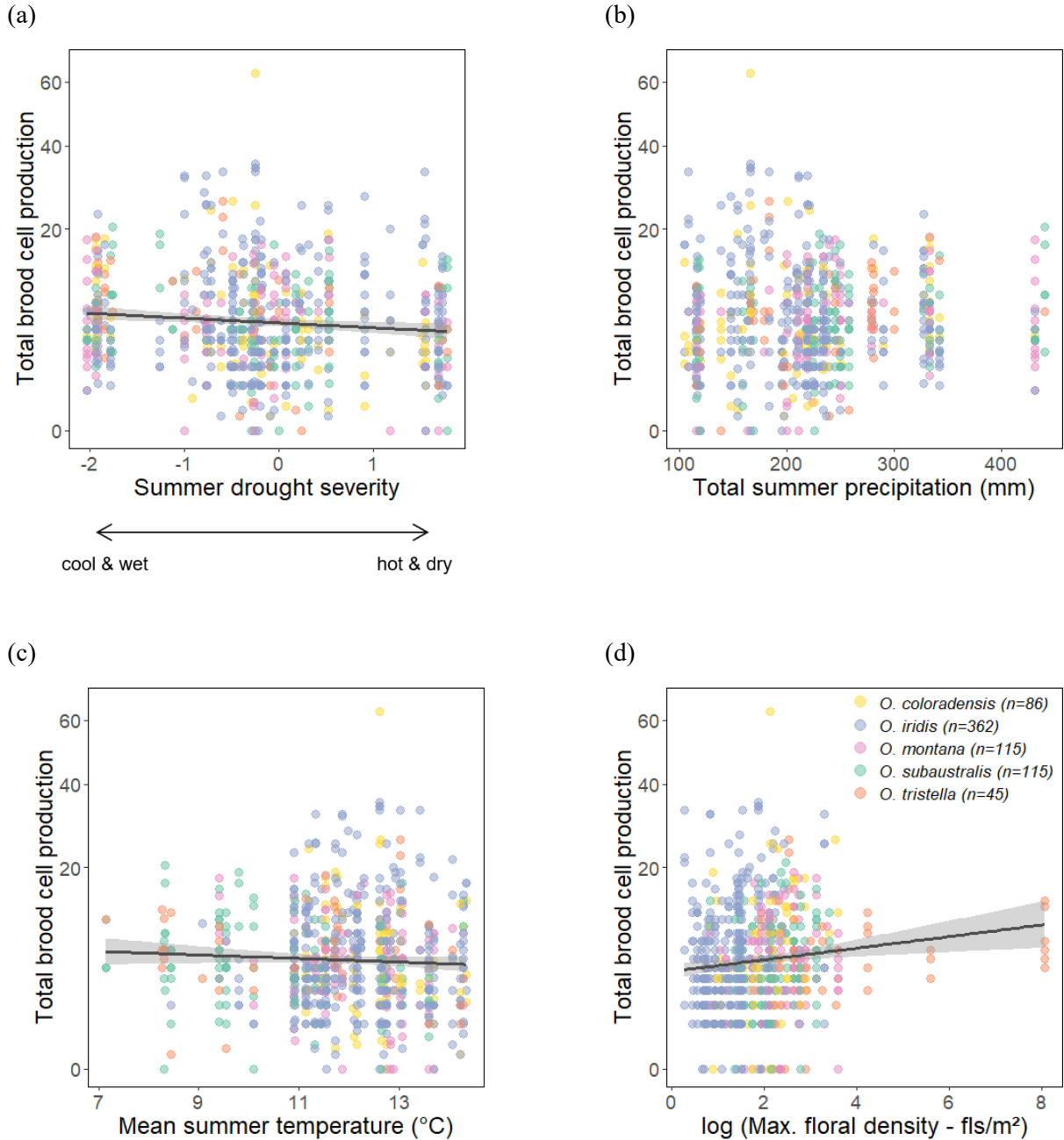
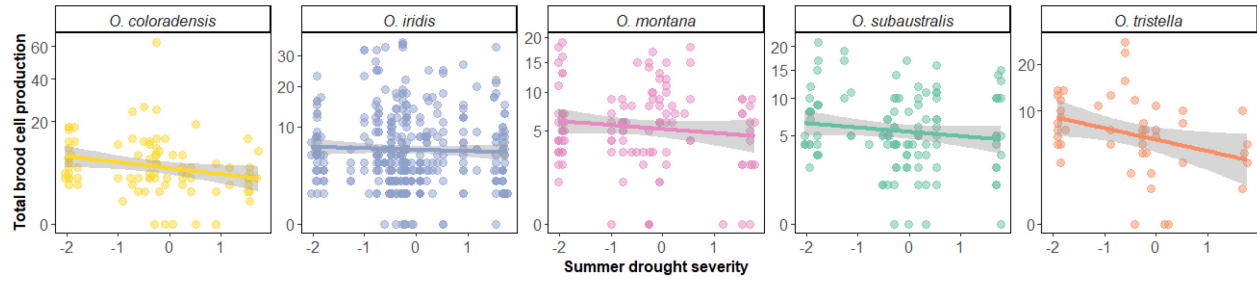


Figure S2. 5. Bee reproductive output figures with outlier individual (Jane) included.

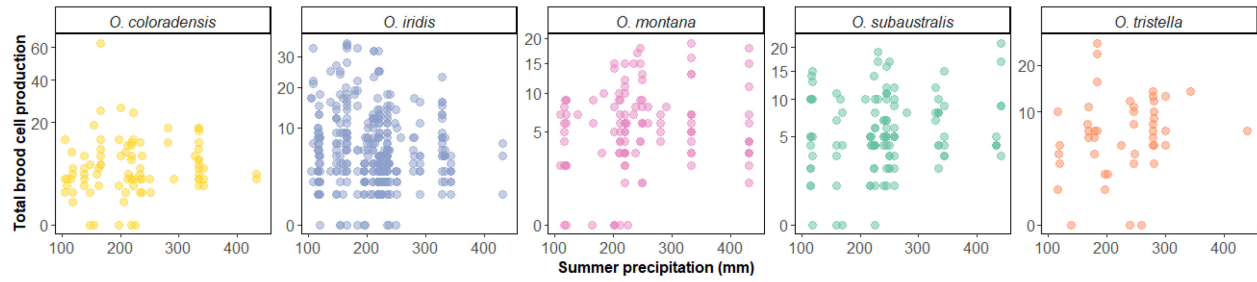
Total brood cell production of individual female bees with outlier included as a function of (a) summer drought severity ($-1 * 4$ -month Standardized Precipitation-Evapotranspiration Index), (b) total summer precipitation, (c) mean summer temperature, and (d) maximum floral density. One *O. coloradensis* individual (“Jane”), observed in 2019 at Brush Creek, produced a total of 63 brood cells (most individuals produced 5 to 9 cells; mean = 7 cells). “Summer” is defined as the period between May and August. Bands indicate 95% confidence intervals for the slope of a simple univariate linear model. Each datapoint represents the total reproductive output of one female bee. Solid lines indicate significant ($p < 0.05$) relationships in the multivariate model described in the text. Note the square-root scaling of the y-axis.

Figure caption on following page

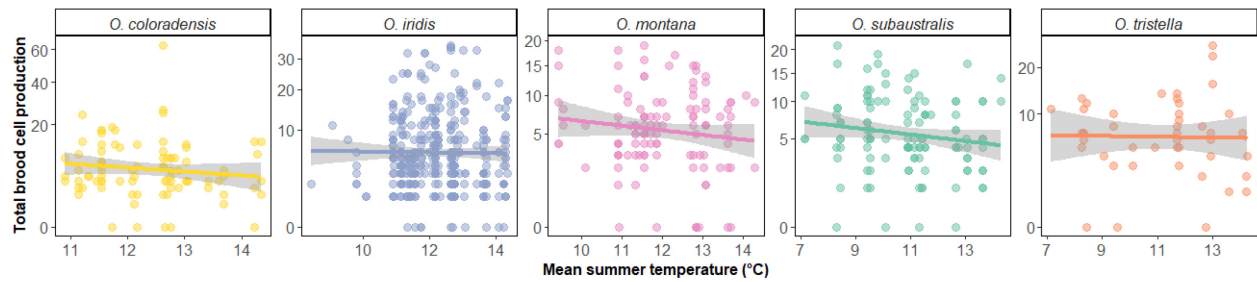
(a)



(b)



(c)



(d)

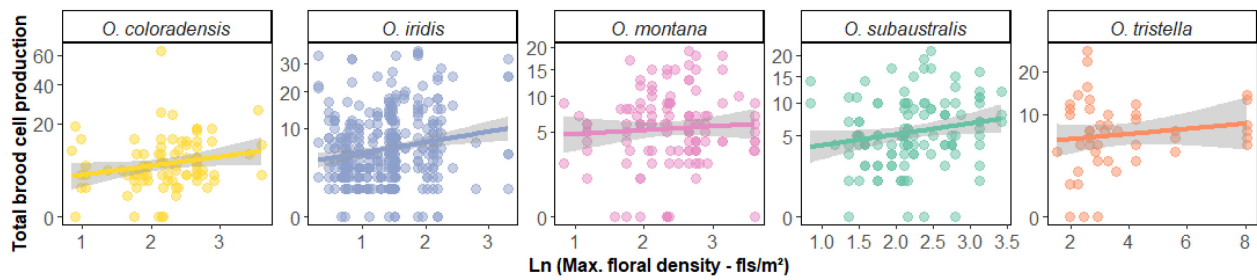


Figure S2. 6. Bee reproductive output figures separated by species.

Total brood cell production of individual female bees separated by species (outlier “Jane” included for *O. coloradensis*) as a function of (a) summer drought severity (-1×4 -month Standardized Precipitation-Evapotranspiration Index), (b) total summer precipitation, (c) mean summer temperature, and (d) maximum floral density (natural log transformed). “Summer” is defined as the period between May and August. Bands indicate 95% confidence intervals for the slope of a simple univariate linear model. Each datapoint represents the total reproductive output of one female bee. Sample sizes as follows: *O. coloradensis*: $n=86$, *O. iridis*: $n=362$, *O. montana*: $n=115$, *O. subaustralis*: $n=115$, *O. tristella*: $n=45$. Solid indicate significant ($p < 0.05$) relationships for the multivariate models described in the text which included all species (i.e., significance is not specific to species). Note the square-root scaling of the y-axis.

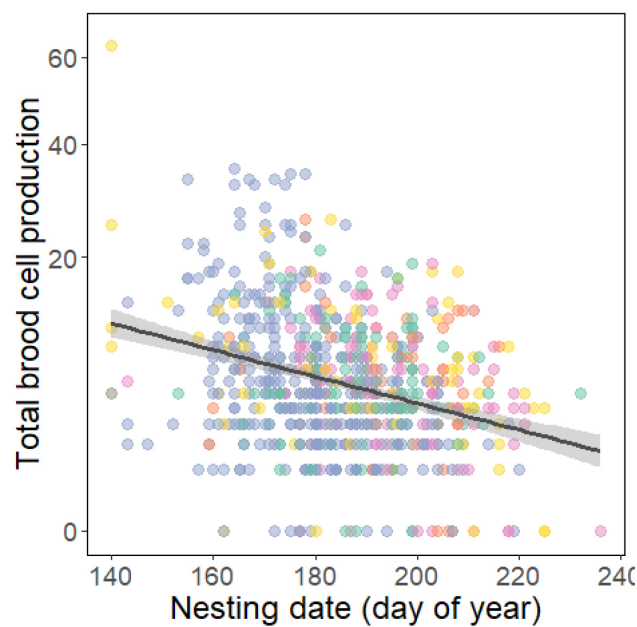


Figure S2. 7. Bee reproductive output vs. nest initiation day.

Total brood cell production of individual female bees (outlier included) as a function of the first day on which individuals were first observed (nesting date). Grey band indicates 95% confidence intervals for the slope of a simple univariate linear model. Each datapoint represents the total reproductive output of one female bee. Sample sizes as follows: *O. coloradensis*: $n=86$, *O. iridis*: $n=362$, *O. montana*: $n=115$, *O. subaustralis*: $n=115$, *O. tristella*: $n=45$. Note the square-root scaling of the y-axis. Day 140 = May 20; day 240 = August 28 in non-leap years.

(a)

	Water-year precipitation	
Water-year precipitation	1.00	Summer temperature
Summer temperature	-0.75	1.00

2013–2022 sites

Max. floral density ~ Precipitation * Temperature + Floral group

(c)

	Nesting date		
Nesting date	1.00	Summer drought severity	
Summer drought severity	-0.26	1.00	Max. floral density
Maximum floral density	0.04	-0.15	1.00

2013–2022 sites

Bee reproductive output ~ Precipitation * Temperature + Nesting date +
Max. floral density

(b)

	Water-year precipitation	
Water-year precipitation	1.00	Summer temperature
Summer temperature	-0.49	1.00

1976–2022 sites

Total floral density ~ Precipitation * Temperature + Floral group

(d)

	Nesting date			
Nesting date	1.00	Summer precipitation		
Summer precipitation	0.26	1.00	Summer Temperature	
Summer Temperature	-0.31	-0.50	1.00	Max. floral density
Maximum floral density	0.04	0.07	-0.02	1.00

2013–2022 sites

Bee reproductive output ~ Summer drought severity + Nesting date + Max. floral density

Figure S2. 8. Pairwise correlations for continuous predictors.

Pairwise correlations between all continuous predictors for models used to analyze relationships between climate variables and floral density (a & b) and bee reproductive output (c & d). (a), (b), (c), and (d) correspond to models 2a, 2b, 3, and 4 in **Table 2.1** of the main text respectively.

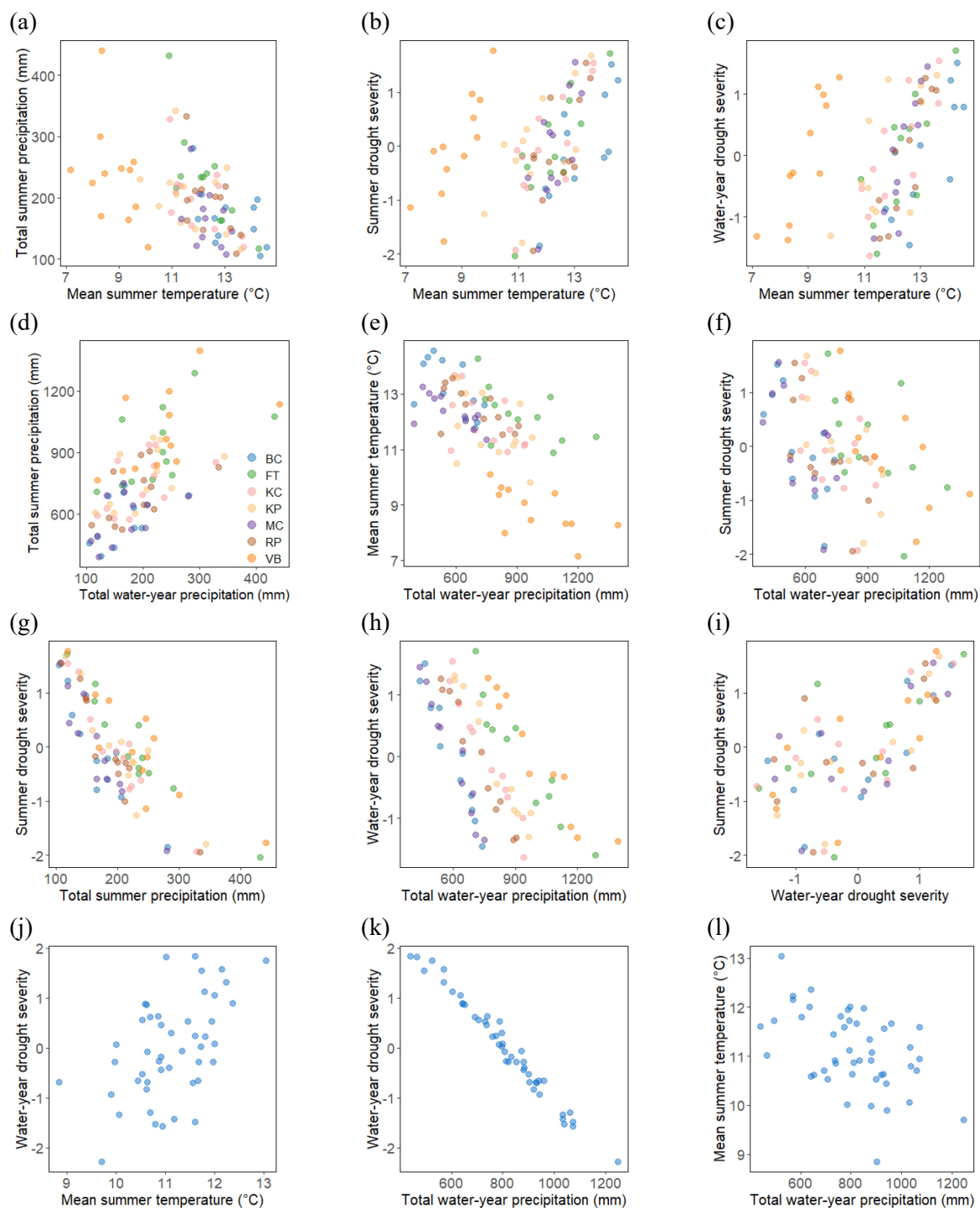


Figure S2. 9. Bivariate relationships between all climate variables.

Relationships between all climate variables at the seven study sites (2013–2022; a–i) and at the RMBL (1976–2022; j–l). For (a)–(i), each datapoint represents climate conditions at a given site in a given year. Site abbreviations in Table S2. 1. For (j)–(l), each datapoint represents climate conditions in a given year. Summer climate variables were not shown for the RMBL as summer climate was used only as a predictor for bee reproductive output (7 sites). Note that the pairs of variables in each plot do not necessarily represent predictors that went into the same model.

Table S2. 4. Results of floral density models.

Results of floral density linear models after non-significant interactions were removed. Models for the 7 sites were linear mixed-effects models (LMMs) and denominator degrees of freedom (df) were estimated using the Satterthwaite approximation (Bates et al., 2015). Models for the RMBL data were simple linear models (LMs). F-values for all models were generated from Type III sums of squares ANOVAs using the “Anova” function in the R package “car” (Fox & Weisberg, 2019). Precipitation and temperature were scaled and centred in all models. Model R²s are marginal R²s for the 7 sites and were generated using the “rsquared.GLMM” function in the R package “MuMIn” (Bartoń 2020). For the RMBL data, R²s are adjusted R²s and were generated using the “lm” function in base R. Bold-face p-values denote significant effects.

Data	Response		Predictors	F	df	p	Model R ²
7 sites	Ln (Max. floral density)	~	Water-year drought severity	5.02	1, 7.3	0.06	0.42
			Floral group + (1 Site) + (1 Year)	75.18	2, 148.7	< 0.01	
7 sites	Ln (Max. floral density)	~	Precipitation (water-year)* Temperature (summer)	6.05	1, 135.1	0.02	0.40
			Floral group + (1 Site) + (1 Year)	76.47	2, 147.8	< 0.01	
RMBL	(Total floral density) ^{0.25}	~	Water-year drought severity	17.84	1	< 0.01	0.78
			Floral group	230.78	2	< 0.01	
RMBL	(Total floral density) ^{0.25}	~	Precipitation (water-year)* Temperature (summer)	12.37	1	< 0.01	0.78
			Floral group	259.50	2	< 0.01	

Table S2. 5. Results of bee reproductive output models.

Results of brood cell production negative binomial generalized linear mixed-effects models (NB-GLMMs) after non-significant interactions were removed. Type II Wald chi-square tests were used to generate Chisq values and assess the significance of model terms using the “Anova” function in the R package “car” (Fox & Weisberg, 2019). Precipitation, temperature and nesting date were scaled and centred in all models. Model R²s are marginal R²s and were generated using the “rsquared.GLMM” function in the R package “MuMIn” (Bartoń 2020).

Data	Response	Predictors	Chisq	df	p	Model R ²
7 sites	Total brood cells ~	Nesting date	111.48	1	<0.01	0.19
		Summer drought severity	5.05	1	0.02	
		Ln (Max. floral density)	13.47	1	<0.01	
		+ (1 Site) + (1 Year) + (1 Species)				
7 sites	Total brood cells ~	Nesting date	111.65	1	<0.01	0.19
		Summer precipitation	< 0.01	1	0.95	
		Summer temperature	4.42	1	0.04	
		Ln (Max. floral density)	15.17	1	<0.01	
		+ (1 Site) + (1 Year) + (1 Species)				

R² values for individual predictors

Table S2. 6. R² values for individual predictors.

R² values for each model predictor. For maximum floral density and total brood cells, R²s are marginal R²s from univariate models (i.e., random effects of species, site and year included). Values were calculated using the “rsquared.GLMM” function in the R package “MuMIn” and univariate models with one predictor at a time (Bartoń 2020). For total floral density, R²s are adjusted R²s from univariate models containing the predictor of interest only. Values were calculated using the “lm” function in base R. Nesting date, precipitation and temperature (water-year and summer) were scaled and centred to mean = 0 and standard deviation = 1 in all models containing these variables. Maximum floral density was natural log-transformed (7 sites), and total floral density was fourth-root transformed (RMBL).

Response	Predictor	R ²
Max. floral density (7 sites)	Water-year Precipitation * Summer Temperature	0.02
	Water-year drought severity	0.02
	Floral group	0.41
Total floral density (RMBL)	Water-year Precipitation * Summer Temperature	0.06
	Floral group	0.76
	Water-year drought severity	0.03
Total brood cells	Summer precipitation	<0.01
	Summer temperature	<0.01
	Summer drought severity	<0.01
	Max. floral density	<0.01
	Nesting date	0.18

Table S2. 7. Results of floral density models (interspecific responses).

Linear model results for the effects of drought severity on floral density at the RMBL when the interactive effect of drought severity and floral group is retained in the model. The overall interactive effect was non-significant, so the results reported in the main text are from a reduced model that did not include this interaction (see Table 2.1 & Table S2. 4). Sums of squares (SS), degrees of freedom (df), F-values and p-values in the upper part of the table were generated from Type III sums of squares ANOVAs using the “anova” function in r with the “type” argument specified to “III” to accommodate interactive effects. Estimates and their associated standard errors (SE) for each floral group are in the lower portion of the table.

	SS	df	F	p
Intercept	57.63	1	2128.12	<0.001
Water-year drought severity	0.01	1	0.35	0.55
Floral group	12.82	2	236.71	<0.001
Water-year drought severity*Floral group	0.15	2	2.68	0.07
Residuals	3.49	129		

	Estimate	SE	t	p
Intercept (Asteraceae)	1.13	0.02	46.13	<0.001
Water-year drought severity	-0.01	0.02	-0.59	0.56
Floral group (Fabeae)	-0.51	0.03	-14.61	< 0.001
Floral group (Generalist)	0.23	0.03	6.67	< 0.001
Water-year drought severity*Fabeae	-0.06	0.03	-1.86	0.07
Water-year drought severity*Generalist	-0.07	0.03	-2.12	0.04

Table S2. 8. Results of bee reproductive output models (interspecific responses).

Negative binomial generalized linear mixed-effects models (NB-GLMMs) results for the effects of summer drought severity on bee brood cell production at the 7 sites with the interaction between drought severity and bee species included. The overall interactive effect of drought severity and bee species was non-significant, so the results reported in the main text are from a reduced model that did not include this interaction (see Table 2.1 & Table S2. 5). χ^2 values, degrees of freedom (df) and p-values were generated from Type III sums of squares ANOVAs using the “Anova” function in the R package “car” (Fox et al. 2001). Estimates and their associated standard errors (SE) for each bee species are in the lower portion of the table and were estimated using the Satterthwaite approximation (Bates et al., 2015).

	χ^2	df	p
Nesting date	129.76	1	<0.001
Summer drought severity	4.83	1	0.03
Bee species	5.70	4	0.22
Maximum floral density	6.18	1	0.01
Summer drought severity * Bee species	7.82	4	0.10

	Estimate	SE	z	p
Intercept (<i>O. coloradensis</i>)	1.74	0.14	12.19	<0.001
Nesting date	-0.40	0.04	-11.39	<0.001
Summer drought severity	-0.32	0.09	-3.45	0.00
Bee species (<i>O. iridis</i>)	-0.07	0.10	-0.72	0.47
Bee species (<i>O. montana</i>)	0.16	0.12	1.36	0.17
Bee species (<i>O. subaustralis</i>)	0.07	0.12	0.58	0.56
Bee species (<i>O. tristella</i>)	-0.10	0.16	-0.61	0.54
Maximum floral density	0.22	0.08	2.65	0.01
Summer drought severity*Bee species (<i>O. iridis</i>)	0.09	0.03	2.49	0.01
Summer drought severity*Bee species (<i>O. montana</i>)	0.20	0.09	2.13	0.03
Summer drought severity*Bee species (<i>O. subaustralis</i>)	0.20	0.09	2.09	0.04
Summer drought severity*Bee species (<i>O. tristella</i>)	0.10	0.13	0.78	0.44

Structural equation model component models

Table S2. 9. Structural equation model component models.

Component models used in climate variable and drought severity structural equation models (SEMs). All models were run as linear mixed effects models (LMMs). Double tildes (~~) denote correlations defined in the model.

SEM	Response	Predictors
Drought severity	Total brood cells	~ Nesting date + Summer drought severity + log (Max. floral density) + (1 Site) + (1 Year) + (1 Species)
	Ln (Max. floral density)	~ Water-year drought severity + (1 Site) + (1 Year) + (1 Floral group) ^a
		~ Water-year drought severity + Summer drought severity + (1 Site) + (1 Year) ^b
	Summer drought severity ~~ Water-year drought severity	
Climate variable	Total brood cells	~ Nesting date + Summer precipitation + Summer temperature + log (Max. floral density) + (1 Site) + (1 Year) + (1 Species)
	Ln (Max. floral density)	~ Water-year precipitation * Summer temperature + (1 Site) + (1 Year) + (1 Floral group)
	Summer precipitation ~~ Summer temperature Summer precipitation ~~ Water-year precipitation Summer temperature ~~ Water-year precipitation	

^a a priori component model

^b revised component model

Supplementary References

- Bartoń, K. (2020). Package “MuMIn.” *R Package Version 1.48.4*. <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Forrest, J. R. K. (2024). Temperature, floral density, and Osmia pollen usage data from seven study sites around the Rocky Mountain Biological Laboratory, Colorado: 2013-2023 ver 4. *Environment Data Initiative*. <https://doi.org/https://doi.org/10.6073/pasta/2992dc076d1c4568afbaa68dcbbaf7dc>
- Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (Third). Sage.

Appendix C - Chapter 3 Supplementary information

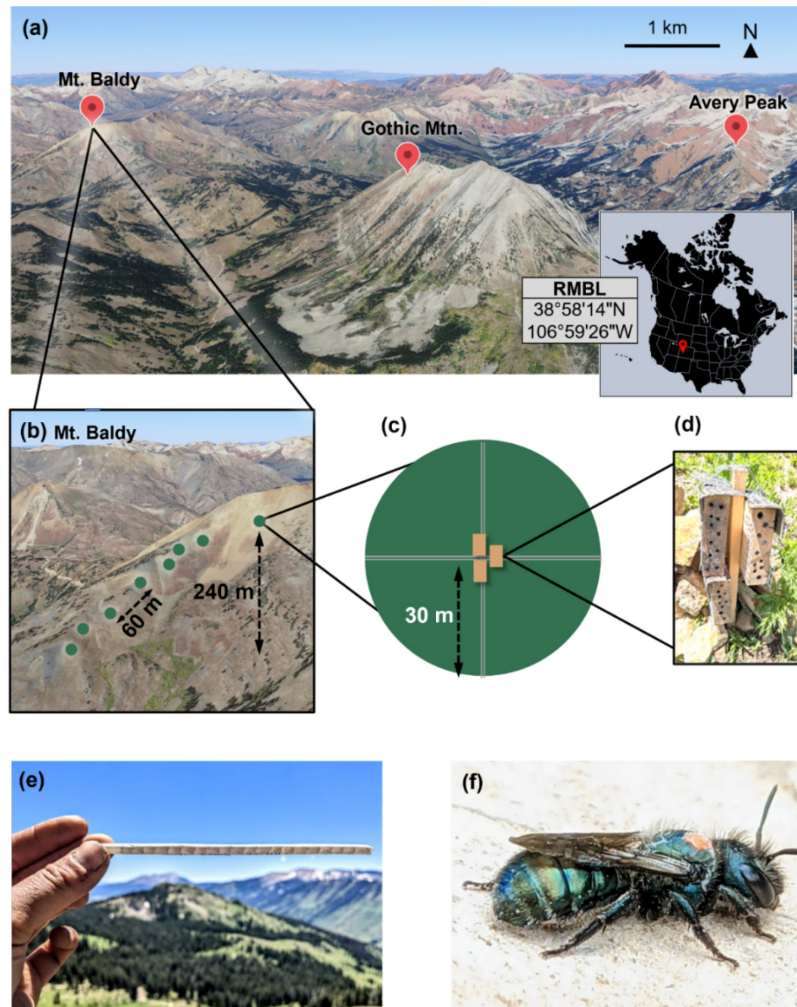


Figure S3. 1. Site locations and study design.

Site locations and study design: (a) locations of three mountains—Mount Baldy, Gothic Mountain, and Avery Peak—near the Rocky Mountain Biological Laboratory in Gothic, Colorado. (b) 8 sites along the slope of Mt. Baldy spanning an elevational gradient of ~240 m (lowest site = 3433 m, highest site = 3677 m). Site centres along the same slope are separated by a minimum walking distance of 60 m. (c) Each site contains three trap-nests at the site centre. Insect surveys were conducted within a 30 m radius of the site centre. Flowers were counted in four 30-m-long transects radiating out from the centre of each site in the four cardinal directions. (d) Three trap-nests consisting of blocks of wood (14 x 2 x 20 cm) with 10–16 holes and roofing material (sheet metal or shingle) affixed to a single wooden stake. Holes were of three diameters: (4.5 mm, 6.1 mm, 8.2 mm). (e) Paper straw containing *O. tristella* nest. Brood cells are visually distinct and can be counted for some species when the straw is held up against the light. This nest contains approximately 20 brood cells. (f) *Osmia tristella* female marked with dot of orange paint on mesosoma. Photo credit: LHW.

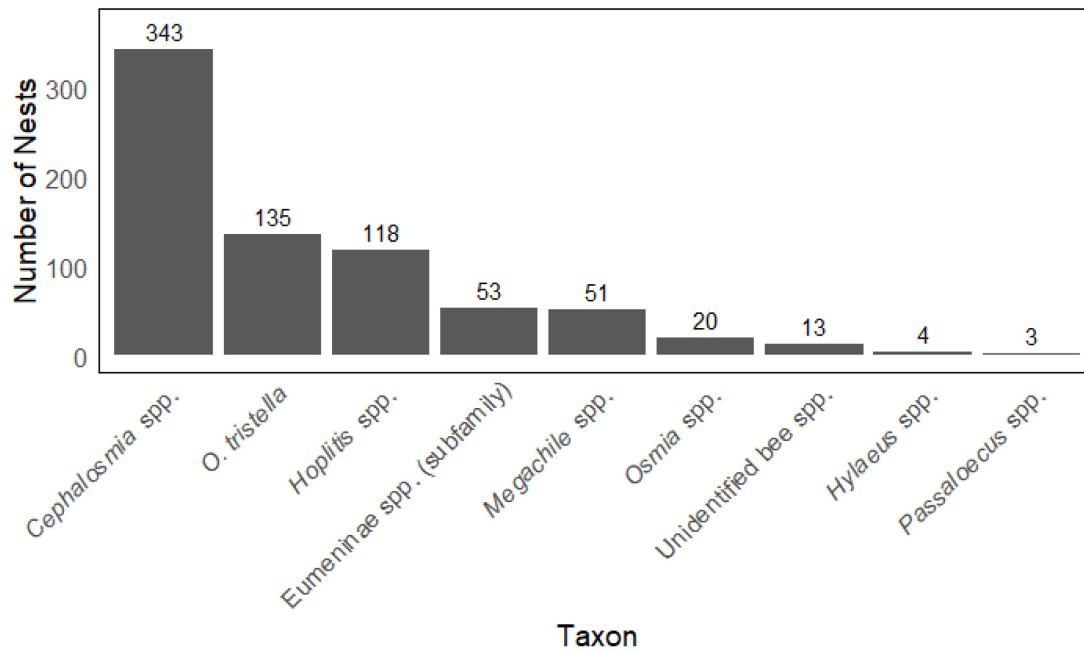


Figure S3. 2. Total number of nests constructed by each taxon.

Number of occupied cavities for each taxonomic group recorded in all trap-nests across all sites and years. For analysis, all *O. montana* and *O. subaustralis* were grouped as *Cephalosmia* (although *O. subaustralis* was much more common). Similarly, we grouped all nests of *H. fulgida* and *H. albifrons* together. Some occupants were identified to genus or subfamily only (i.e., *Eumeninae*, *Megachile*, *Hylaeus*, *Passaloecus*). The numbers of nests reported here do not correspond exactly to those reported in the text with respect to the relationship between elevation and number of brood cells; in some cases, females constructed nests in cavities that lacked paper straws (birds often extracted straws between site visits); we were sometimes able to determine the taxonomic identity of the occupant upon encountering them at our sites, but could not quantify their brood cell production without the straw. In other cases, the taxonomic identities of the occupants were ambiguous because the occupant was never sighted before the nest was sealed. These nests were identified as “*Osmia* spp.” and “Unidentified bee spp.” based on the construction of the nest entrance seal. There were also cases where nests that were built in straws were completely destroyed by animals leaving behind insufficient amounts of wall material to identify the occupant. Nests were also occasionally abandoned by the occupant with only a single wall. The occupant identity of nests for which wall material was clearly made primarily up of masticated leaf material were recorded as “*Osmia* spp.”, while those for which we did not have sufficient information were recorded as “Unidentified bee spp.” (wood-nesting wasps constructed distinct nests). Nests for which the occupant identity remained ambiguous were not included in our analysis with brood cells per nest but were included in counts of nests per site.

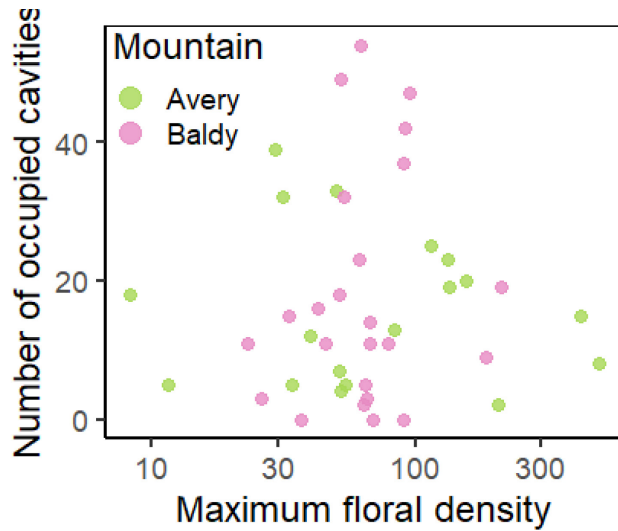


Figure S3. 3. Number of occupied cavities vs. floral density.

Number of occupied cavities as a function of maximum floral density at 14 sites from 2021 to 2023. Each datapoint represents the total number of cavities occupied by wood-nesting bees and wasps at a given site on one of two mountains in a given year of the study (floral density was not quantified at the sites on Gothic Mountain; see Table S3. 1). $n = 18$ and 24 unique year-mountain-site combinations for Avery and Baldy respectively. Maximum floral density was not a significant predictor of the total number of occupied cavities (see main text). Datapoints were jittered for visualization. Note the $\log_{10}$ -scaling of the x-axis.

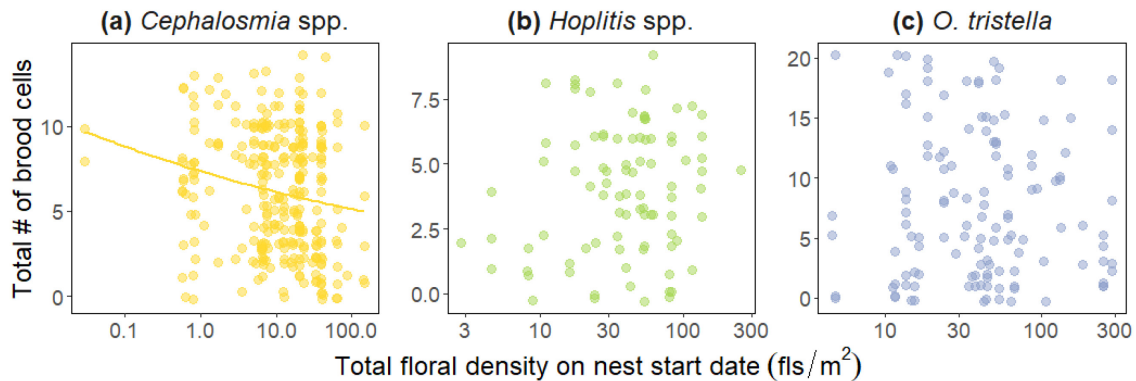


Figure S3. 4. Brood cells per nest vs. floral density.

Number of brood cells per nest for (a) *Cephalosmia* spp. (*Osmia subaustralis* and *O. montana*), (b) *Hoplitis* spp. (*H. albifrons* and *H. fulgida*), and (c) *Osmia tristella* as a function of total floral density at 14 sites from 2021 to 2023. Each datapoint represents one nest constructed by an individual of one of three species at a given site on one of three mountains in a given year of the study. Sample sizes for (a), (b), and (c) are as follows: $n = 336$, 118, and 134 nests respectively. Solid lines indicate significant ($p < 0.05$) relationships in models run separately for each taxonomic group. Note that in the model reported in the text, all three taxonomic groups were included in the same model and the lines (or lack thereof) are for visualization only. Datapoints are jittered.

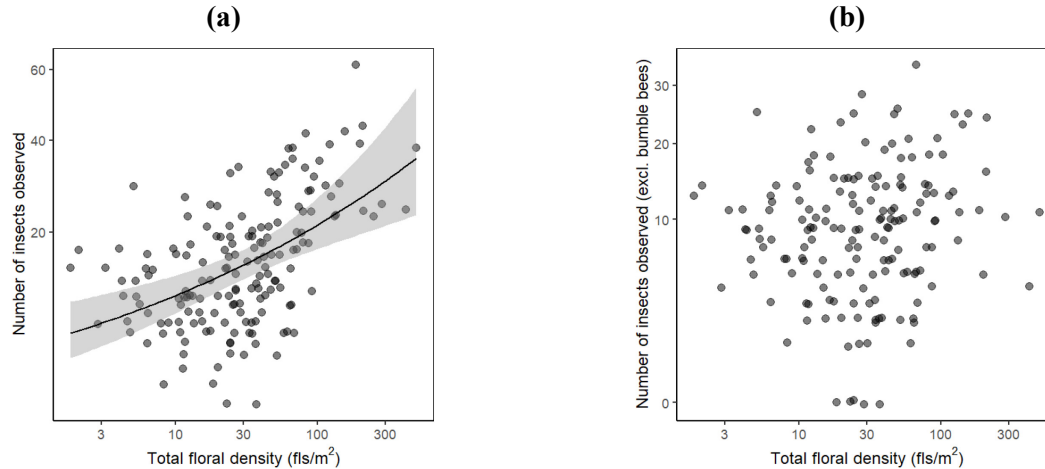


Figure S3. 5. Bee and wasp abundance vs. floral density.

Number of all bees and wasps (wood- and ground-nesting combined) observed during insect surveys including bumble bees (a) and excluding bumble bees (b) as a function of total floral density. Each datapoint represents the total number of bees and wasp observed during a 30-minute survey period. $n = 169$ surveys at 14 sites (2 mountains) and 3 years. The solid line in (a) denotes the significant ($p < 0.05$) relationship in the multivariate model described in the text and the grey band represents 95% confidence interval for the slope of a simple univariate linear model. Datapoints were jittered and the x and y-axes were log₁₀ and square-root transformed respectively to better visualize all points and trends in the data.

Table S3. 1. Site information.

Mountain names, years in which they were monitored, number of sites, elevational range of sites, and data collected.

Mountain	Years monitored	# of sites	Elevational range (m)	Data collected	
				Trap-nest activity	Insect & flower surveys
Avery Peak	2021–2023	6	3457–3638	X	X
Mount Baldy	2021–2023	8	3443–3677	X	X
Gothic Mountain	2022–2023	5	3580–3717	X	

Table S3. 2. List of plant taxa surveyed.

List of plant taxa counted during flower surveys and the floral units quantified. Not all taxa were present at each site.

Plant taxon	Unit counted
<i>Achillea millefolium</i>	Stalks (Flowering stems)
<i>Agoseris glauca</i>	Capitula
<i>Antennaria parvifolia</i>	Stalks (Flowering stems)
<i>Aquilegia coerulea</i>	Flowers
<i>Arctostaphylos uva-ursi</i>	Flowers
<i>Arnica rydbergii</i>	Capitula
<i>Boechera stricta</i>	Flowers
<i>Campanula rotundifolia</i>	Flowers
<i>Castilleja occidentalis</i>	Stalks (Flowering stems)
<i>Chaenactis douglasii</i>	Capitula
<i>Cymopterus lemmonii</i>	Stalks (Flowering stems)
<i>Delphinium barbeyi</i>	Flowers
<i>Eremogone congesta</i>	Flowers
<i>Erigeron</i> spp.	Capitula
<i>Eriogonum umbellatum</i>	Stalks (Flowering stems)
<i>Erysimum capitatum</i>	Flowers
<i>Fragaria virginiana</i>	Flowers
<i>Geranium viscosissimum</i>	Flowers
<i>Hedysarum boreale</i>	Flowers
<i>Helianthella quinquenervis</i>	Capitula
<i>Heterotheca villosa</i>	Capitula
<i>Hymenoxys hoopesii</i>	Capitula
<i>Ipomopsis aggregata</i>	Flowers
<i>Ivesia gordonii</i>	Stalks (Flowering stems)
<i>Lathyrus lanszwertii</i>	Flowers
<i>Ligusticum porteri</i>	Area ¹
<i>Linum lewisii</i>	Flowers
<i>Lupinus</i> spp.	Flowers
<i>Maianthemum stellatum</i>	Stalks (Flowering stems)
<i>Oreochrysum parryi</i>	Capitula ²
<i>Oxytropis deflexa</i>	Flowers
<i>Pedicularis bracteosa</i>	Stalks (Flowering stems)
<i>Penstemon crandallii</i>	Flowers
<i>Penstemon whippleanus</i>	Flowers

Table S3. 2. Continued:

Plant taxon	Unit counted
<i>Phacelia hastata</i>	Flowers
<i>Phacelia sericea</i>	Flowers
<i>Potentilla</i> spp.	Flowers
<i>Ribes montigenum</i>	Flowers
<i>Rosa woodsii</i>	Flowers
<i>Sedum integrifolia</i>	Stalks (Flowering stems)
<i>Senecio crassulus</i>	Capitula
<i>Senecio</i> spp.	Stalks (Flowering stems)
<i>Solidago</i> spp.	Stalks (Flowering stems)
<i>Taraxacum officinale</i>	Capitula
<i>Tragopogon</i> spp.	Capitula
<i>Vaccinium myrtillus</i>	Flowers
<i>Valeriana acutiloba</i>	Stalks (Flowering stems)
<i>Valeriana occidentalis</i>	Stalks (Flowering stems)
<i>Vicia americana</i>	Flowers
<i>Viola adunca</i>	Flowers
<i>Viola praemorsa</i>	Flowers

¹ Number of Canadian two-dollar coins that can be fit on the umbel when the umbel is condensed such that there are no longer spaces between the umbelets

² May have been mistakenly recorded as "*Senecio*" in 2021

Table S3. 3. List of bee and wasp taxa identified.

List of bee and wasp taxa identified in the field during insect surveys, nesting habits, and notes concerning ambiguity around taxonomic identifications and nesting habits.

Taxon	Taxonomic rank	Nesting habit	Notes (e.g., ambiguous nesting habit)
<i>Agapostemon</i> sp.	Genus	Ground	
<i>Ammophila</i> sp.	Genus	Ground	
<i>Ancistrocerus</i> sp.	Genus	Wood	
<i>Andrena</i> sp.	Genus	Ground	
<i>Anthophora urbana</i>	Species	Ground	
<i>Bembix</i> sp.	Genus	Ground	
<i>Bombus</i> sp.	Genus	Ground	
<i>Bombus appositus</i>	Species	Ground	
<i>Bombus flavidus</i> ssp. <i>flavidus</i>	Subspecies (of <i>Bombus flavidus</i>)	Ground	
<i>Bombus flavifrons</i>	Species	Ground	
<i>Bombus insularis</i>	Species	Ground	
<i>Bombus nevadensis</i>	Species	Ground	
<i>Bombus occidentalis</i>	Species	Ground	
<i>Bombus sylvicola</i>	Species	Ground	
<i>Coelioxys</i> sp.	Genus	Wood	<i>Coelioxys</i> spp. are kleptoparasites on <i>Megachile</i> spp., possibly including <i>M. melanophaea</i> (see notes below)
<i>Colletes</i> sp.	Genus	Ground	
<i>Dialictus</i>	Subgenus (of <i>Lasioglossum</i>)	Ground	
<i>Dolichovespula maculata</i>	Species	Ground	
<i>Dufourea maura</i>	Species	Ground	
<i>Dufourea</i> sp.	Genus	Ground	
<i>Eumeninae</i>	Subfamily	Wood	
<i>Halictidae</i>	Family	Ground	
<i>Halictus</i> sp.	Genus	Ground	
<i>Hoplitis fulgida</i>	Species	Wood	
<i>Hylaeus</i> sp.	Genus	Wood	<i>Hylaeus</i> species frequently nest in plant stems (personal observations)
<i>Lasioglossum</i> sp.	Genus	Ground	
<i>Megachile</i> sp.	Genus	Wood	Some of these observations may have been of <i>M. melanophaea</i> (ground-nesting <i>Megachile</i>).
<i>Melanosmia</i>	Subgenus (of <i>Osmia</i>)	Wood	
<i>Nomada</i> sp.	Genus	Ground	
<i>Osmia</i> sp.	Genus	Wood	
<i>Osmia bucephala</i>	Species	Wood	
<i>Panurginus</i> sp.	Genus	Ground	
<i>Podalonia</i> sp.	Genus	Ground	
<i>Pseudomasaris</i> sp.	Genus	Ground	
<i>Pseudomasaris marginalis</i>	Species	Ground	
<i>Pyrobombus</i>	Subgenus (of <i>Bombus</i>)	Ground	
<i>Sphecidae</i>	Family	Ground	
<i>Sphecodes</i> sp.	Genus	Ground	
<i>Sphex</i> sp.	Genus	Ground	
<i>Stelis</i> sp.	Genus	Wood	
<i>Tachysphex</i> sp.	Genus	Ground	
<i>Vespula</i> sp.	Genus	Ground	
<i>Vespula atropilosa</i>	Species	Ground	
<i>Xanthosarus</i> sp.	Subgenus (of <i>Megachile</i>)	Wood	Some of these observations may have been of <i>M. melanophaea</i> (ground-nesting <i>Megachile</i>).

Table S3. 4. iNaturalist photo identifiers.

Individuals who identified photos of observed bees and wasps on iNaturalist and the number of identifications contributed. Names for some users were not available.

iNaturalist username	Name	# of identifications
bclaridge	Brandon Claridge	26
bdagley	Brian Dagley	6
behm Rachel	Rachel Behm	1
cecildomyidae	Cecil Smith	4
frank_hornig		1
humanbyweight	Chris Alice "Alie" Kratzer	1
hymenopterater		11
jessmullins	Jessica Mullins	37
johnascher	John Ascher	112
juan_sphex	Juan C. Espinosa	1
matthias22	Matthias Buck	2
morcutt	Michelle Orcutt	1
nmdg	Nathaniel Green	2
susanna_h	Susanna Heideman	19
sydneygram	Sydney Gram	2
villu	Villu Soon	1
xianzx	Xian Zhou	2

Table S3. 5. Study environmental impacts and mitigation strategies.

Environmental impacts of activities directly associated with conducting this study and measures taken by the authors to mitigate them. The list of environmental impacts is not exhaustive. See Grogan (2021) for more information.

	Activity	Environmental impact	Mitigation strategies
Travel	Transport to field station ~6000 km round trip between Ottawa, Ontario to Gothic, Colorado $6000 * 3 \text{ years} = \sim 18\,000 \text{ km}$	Fossil fuel emissions, production of tire wear particles, collision with flying insects.	Travelled by car with up to 3 people per vehicle instead of flying and took the most direct route possible. In 2023, travelled in an electric vehicle.
Travel	Transport between field station (RMBL) and sites throughout each field season ~50 km round trip between RMBL and base of Mt. Baldy ~30 trips made $50 * 30 \text{ trips} = \sim 150 \text{ km}$	Fossil fuel emissions, production of tire wear particles, collision with flying insects.	Minimized number of trips per field season by camping overnight at sites in order to complete more sampling per trip. Established one set of sites (Avery Peak) within walking distance of RMBL.
Sampling	In 2021, 20 insects (bees and wasps) were euthanized as voucher specimens during insect surveys	Loss of 20 individuals from the environment.	Discontinued this practice after 2021. Focused on capturing photos and uploading them to iNaturalist for ID instead given that species-level identifications were not necessary.
Materials	57 trap-nests were constructed using SPF wood and fitted roofing material (sheet metal or asphalt shingles). The trap-nests were mounted on 2"x2" stakes	Resource extraction for raw materials and fossil fuel emissions to process them and transport them to distribution centres.	Some trap-nests were re-used from previous projects in the lab. Sheet metal, shingles, and wooden stakes were discarded materials found in local waste receptacles. Typically travelled by bike or public transit to obtain materials.

References

Grogan, Paul. "Raising awareness of science's environmental footprint." *Frontiers in Ecology & the Environment* 19, no. 3 (2021).

Appendix D - Chapter 4 Supplementary information

Supplementary methods

Site selection

Following our call for participants interested in hosting trap-nests in their gardens, we received 27 and 46 expressions of interest from Ottawa and Toronto, respectively. To select sites, we first characterized the temperature conditions of each potential site by calculating the mean land surface temperature (LST) within a 1 km radius of the site. Surface temperature was derived from Landsat 8 (Level 1) thermal imagery taken on June 18, 2020, for sites in Ottawa, and June 16, 2020, for sites in Toronto. Level 2 data (which have undergone further pre-processing and were used for generating LST values in analysis; see below) were not yet available at the time of site selection. Land surface temperature was derived following the formulas outlined by (Avdan and Jovanovska 2016). For Ottawa and Toronto, we iteratively generated sets of 15 and 16 sites respectively from the pools of potential sites and selected the set for which variation in land surface temperature would be maximized and spatial autocorrelation (Moran's I) minimized. Zonal statistics (to calculate LST), and spatial autocorrelation were calculated in ArcGIS Pro (version 2.5; Esri Inc. 2020).

Some sites comprised 2-3 “sub-sites”, with trap-nests being placed in the gardens of multiple residents but within the same 1 km radius, generally no more than 300 m apart (Table S4. 1). This occurred because some residents indicated that they could no longer participate in the study part-way through the 3 years of data collection and we had to find another resident within the same area to participate. All sub-sites within a given site were represented by the same LST.

Trap-nest design

The first trap-nest design consisted of 14 cm blocks of 3.8 cm x 18 cm SPF wood with eight grooves cut into each flank (total of 16 grooves, i.e., cavities). Grooves were of three different widths to accommodate different taxa. Each trap-nest had 4 large cavities (8 mm diameter), 8 medium cavities (6.4 mm), and 4 small cavities (4.5 mm). A plexi-glass panel was affixed to each flank of the trap-nest to create closed cavities. Small planks of wood were attached to the tops and bottom of blocks to serve as roofs and bases. Panels of 1/8” wood board cut to the size of each trap-nest flank were nested between the roof and base pieces and could be slid open and shut to temporarily view trap-nest contents. In 2021, all trap-nests were designed in this way, and each site had two trap-nests. In 2022 and 2023, 1–2 trap-nests of a different design were added to most sites because occupancy in the trap-nests in 2021 was relatively low. These additional trap-nests consisted of 3.8 cm x 14 cm SPF wood with 10–12 holes drilled 14 cm deep. Holes were of the same diameters as in the first design and were lined with paper straw liners so that nests could be extracted. A section of shingle was affixed to the top of trap-nests to serve as a roof. In both designs, a 10 mm x 4.5 mm hole was drilled into the back of each trap-nest to accommodate an iButton datalogger which was concealed by a thin piece of wooden board screwed to the back of each trap-nest following their deployment.

Calculating land surface temperature

Level 2 Landsat data were available shortly after site selection and were used to derive the land surface temperature (LST) values used in analysis. LST values were calculated by applying the following formula (from EROS 2020):

$$\text{Surface temperature} = (DN * 0.00341802) + 149.0$$

Where, DN is the digital number from Band 10 of the raster file, and 0.0341802 and 149 are scaling factors. We then converted the resulting values from degrees Kelvin to degrees Celsius by subtracting 273.15.

Overwintering developing brood

Developing brood from 2021 were overwintered in sealed containers outdoors. Brood from 2022 and 2023 were overwintered in an incubator set to 4 °C. Incubator temperatures were gradually increased to 23°C over a one-month period beginning in mid-April.

Table S4. 1. Site information.

Site names, and site-specific information on sub-sites (see “Site selection”), garden types, years active etc.

City	Site	Garden type	Notes
Ottawa	ANNA	Residential garden	
Ottawa	BARR	Residential garden	This site was added in 2022 and comprised two sub-sites: MARY and NANC
Ottawa	BERI	Residential garden	
Ottawa	BREN	Residential garden	
Ottawa	CHLO	Residential garden	
Ottawa	FLET	Community garden	
Ottawa	HEAT	Residential garden	
Ottawa	HILA	Residential garden	
Ottawa	IOLA	Residential garden	
Ottawa	JUDI	Residential garden	
Ottawa	JULI	Residential garden	
Ottawa	MARI	Residential garden	
Ottawa	MARW	Residential garden	
Ottawa	MELA	Residential garden	Resident participated in 2021, withdrew in 2022, and rejoined in 2023
Ottawa	OOEA	Community garden	This site comprised two sub-sites: CHIL and CARO
Ottawa	ROBL	Residential garden	
Toronto	BRUC	Residential garden	
Toronto	CLIF	Residential garden	This site comprised two sub-sites: DORT and LIND
Toronto	DAWN	Residential garden	
Toronto	HARO	Residential garden	
Toronto	ISLA	Residential garden	This site comprised two sub-sites: REIK and CARU
Toronto	JIMB	Residential garden	
Toronto	JOAN	Residential garden	
Toronto	JUNC	Residential garden	This site comprised two sub-sites: DILY and GABR
Toronto	KATH	Residential garden	
Toronto	MIRI	Residential garden	
Toronto	RICH	Residential garden	
Toronto	SAYE	Residential garden	
Toronto	SPAD	Residential garden	This site comprised two sub-sites: HVRA and HOME
Toronto	TOMC	Residential garden	
Toronto	TOMM	Residential garden	

Table S4. 2. Thermal imagery dates.

Thermal imagery dates (days) for each month in each year of the study. Landscape temperatures (land surface temperature) reflect temperature conditions on these dates.

	2021					2022					2023				
City	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep
Ottawa	13	^a NA	23	24	25	7	25 ^b	3 ^c	19	29	26	3	5	6	15
Toronto	18	12	5	31	7	30	23	9	18	2	25	17	20	20	22

^a All available images in June 2021 for the Ottawa area had exceedingly high cloud cover

^b Landscape temperature for 1 site (ROBL) in June 2022 reflect conditions on June 24th.

^c Landscape temperatures for 1 site (ROBL) in Ottawa in July 2022 reflect conditions on July 2.

Table S4. 3. Summary of microhabitat variables.

Spring measurements occurred between April and May. Fall measurements occurred between August and October.

Microhabitat feature	Season measured	Description	Notes
Water feature index	Spring	Ratio of the water area to the square of the shortest straight-line distance between the front of the trap-nest and the water feature (water area / distance ²). Water depth was not accounted for.	At some sites, trap-nests were placed in both the front and rear lots of properties (i.e., they were separated by a house). Water indices were only calculated between trap-nests and water features that occurred in the same lot.
Light intensity	Installed in the spring during trap-nest set-up	Mean light intensity in June (Lux); measured using light intensity loggers (Onset HOBO UA-002-64 Pendant Temperature/Light Data Logger) placed facing upwards on the roofs of trap-nests.	Full-season light data were only captured for 78 out of the 274 trap-nests set out (29%) over the 3 years due to inadequate numbers of loggers. We used June data only to ensure that we were capturing light conditions after spring leaf-out.
Maximum vegetation height and identity	Fall	Height of the tallest vegetative growth within a 1 m radius of each trap-nest. If the height of the maximum growth was > 2 m (e.g., trees or tall shrubs), we used the mobile application “Arboreal” (https://arboreal.se/) to estimate height. Due to some uncertainty with the application accuracy at the time of use, we rounded values down to the nearest 0.5 m.	Maximum vegetation heights were recorded for 210/274 (76.6%) of trap-nests. Heights were not recorded for most trap-nests in 2021.
Pervious surface area	Spring (2022), Fall (2023)	A single observer stood as close to the trap-nest as possible and took four photos of the ground directly in front, behind, to the left, and to the right of trap-nest holding the camera with their arm completely outstretched at shoulder height. The percentage of each photo covered by impervious surfaces (e.g., asphalt, paving stones, bricks, gravel, deck boards etc.; see supplementary material for classifications) was determined using imageJ, and averaged across all four images for each trap-nest.	See Figure S4. 2 for examples of photos.

Table S4. 4. Correlation matrix for microhabitat variables.

Pearson correlation matrix for four variables characterizing the microhabitat surrounding trap-nests as well as mean summer nest temperature. Microhabitat variables are described in Table S4. 3.

	Mean summer nest temperature	Maximum vegetation height (1 m)	Percent pervious area (1 m)	Mean light intensity (June)	Water index
Mean summer nest temperature	1				
Maximum vegetation height (1 m)	-0.14	1			
Percent pervious area (1 m)	-0.31	-0.06	1		
Mean light intensity (June)	0.53	-0.26	-0.31	1	
Water index	0.03	0.04	-0.07	0.03	1

Table S4. 5. Summary of statistical models.

Predictors and covariates in bold were retained in the final model; those in grey were removed as their effects on the response were non-significant. Variables were transformed, scaled or centred as described in the main text.

Objective addressed	Response variable	Main predictors of interest	Covariates	Each datapoint represents
1	Juvenile mass	~ Mean summer nest temperature	Cavity size Cell position 1 taxon 0 + nest temperature taxon 1 site / trap-nest ID / cavity City Year Box design Date cocoon weighed	One juvenile bee or wasp
2	Daily mean nest temperature	~ 1 km Land surface temperature * Maximum vegetation height * Month ²	Year (factor) Box design Month Month² 1 site / trap-nest ID City Trap-nest height Trap-nest direction	Daily mean temperature in a trap-nest on a single day of the year (each trap-nest represented by 5 values per year, one for each month from May–September)

Table S4. 6. Average summer temperatures from local weather stations.

Average summer temperatures (May–September) from local weather stations in Toronto and Ottawa, ON, Canada over the three years of the study compared to 30-year averages. Data retrieved from Environment Climate Change Canada.

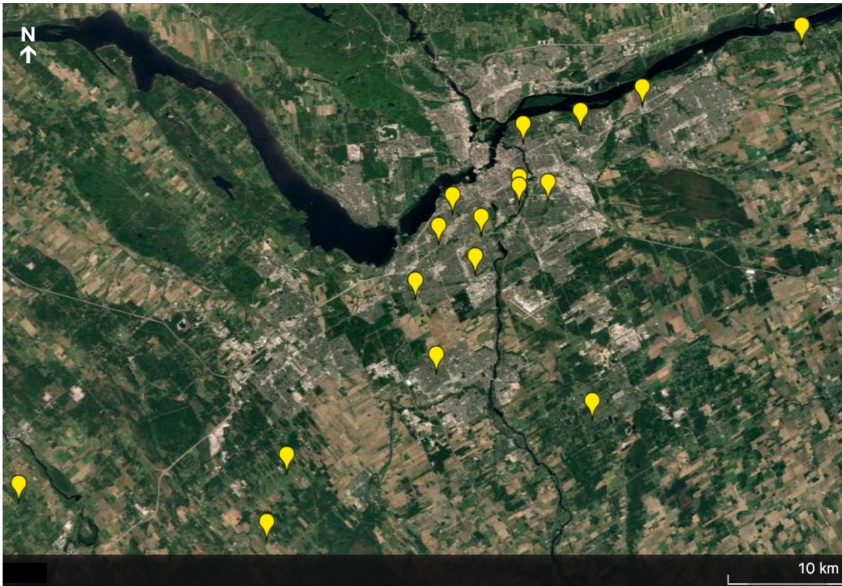
	30-year average (1991-2020)	2021	2022	2023
Toronto	19.3°C	20.0	19.9	19.3
Ottawa	17.9°C	18.3	17.9	17.8

Table S4. 7. Proportion of variance explained by random effects.

Proportion and percentage of total variance of random effects explained by each random effect term in the model used to test Objective 1.

Random effect term	Proportion of variance explained
Taxon (intercept)	0.480 (72.62%)
0 + Nest temperature Taxon (slope)	0.022 (3.39%)
Cavity / Trap-nest / Site	0.126 (19%)
Trap-nest / Site	0.031 (4.69%)
Site	0.002 (0.29%)
Total random effect variance:	0.6614

(a)



(b)

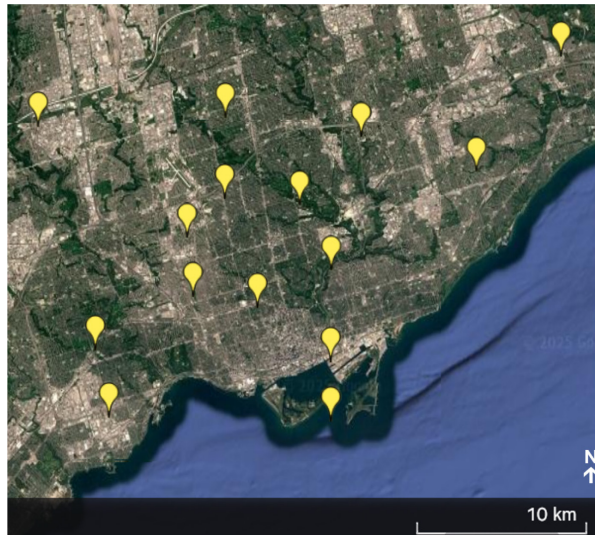


Figure S4. 1. Site locations.

Locations of study sites in (a) Ottawa, Ontario, Canada and (b) Toronto, Ontario, Canada.

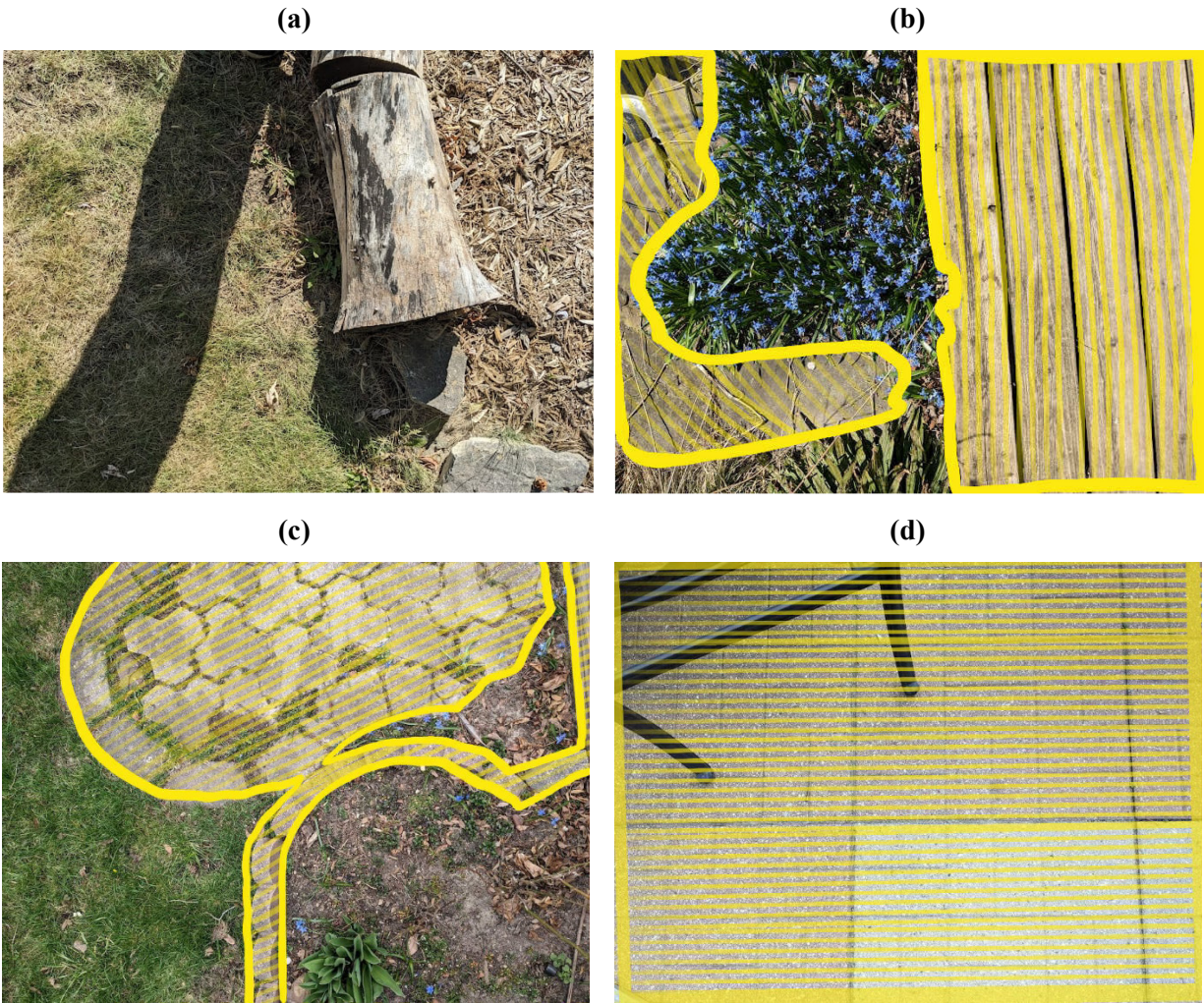


Figure S4. 2. Impervious surface area photos.

Sample photos of the ground surrounding trap-nests with (a) 100%, (b) 35%, (c) 52%, and (d) 0% pervious surface area. Grass, shrubs, bare ground, topsoil, wood or leaf litter mulch, and logs were considered “pervious”. Asphalt, pavement, paving stones, bricks, gravel, deck and fence boards, sheet metal and plastic were considered “impervious”. Percent pervious surface area was characterized in ImageJ (<https://ij.imjoy.io/>).

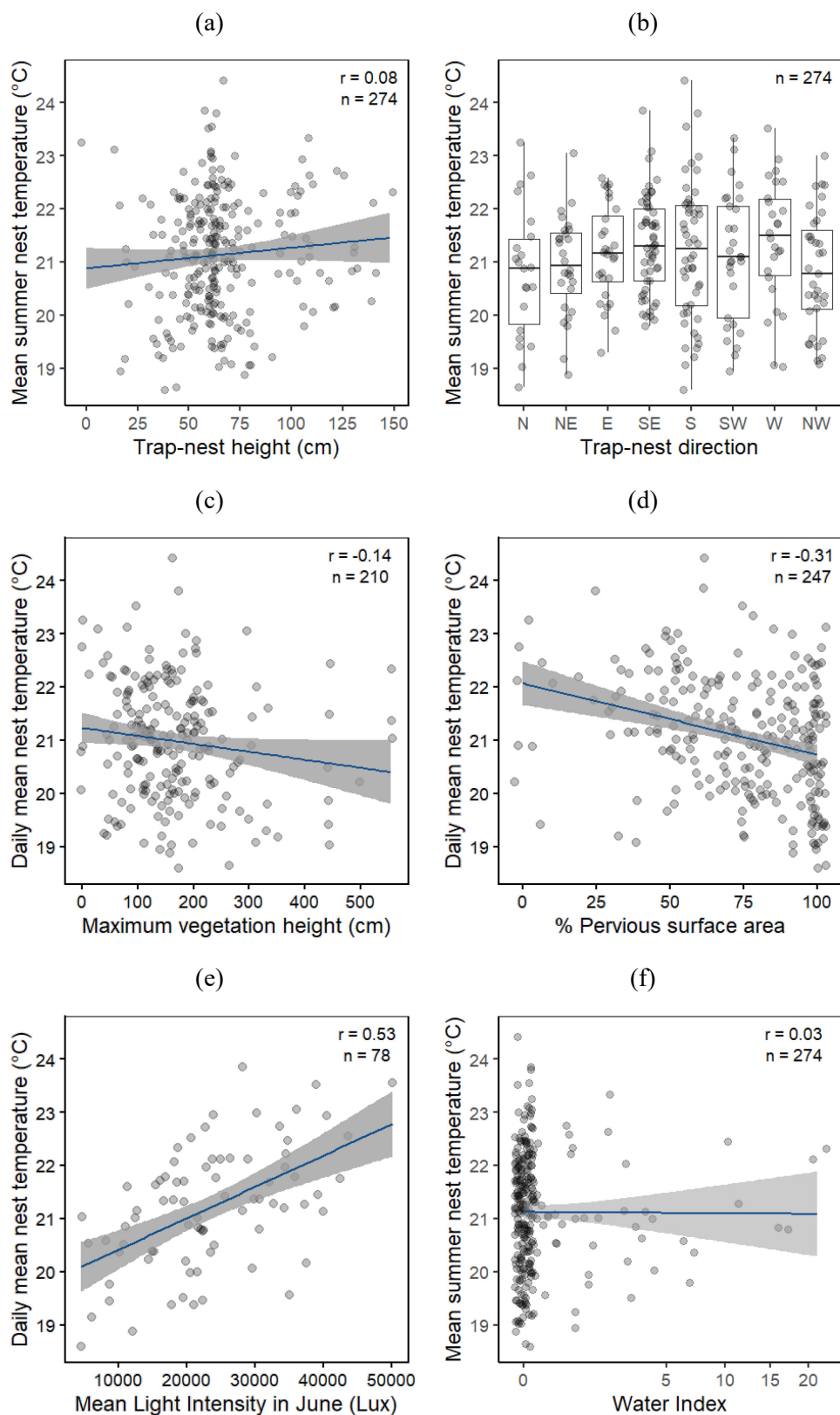
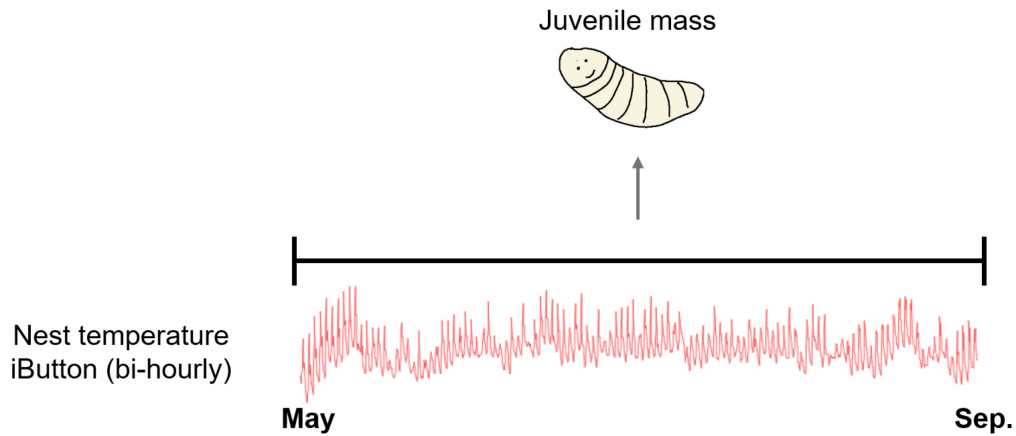


Figure S4. 3. Relationship between trap-nest microhabitat and nest temperature.

Relationships between mean summer nest temperature and: (a) trap-nest height (i.e., distance between ground and bottom corner of trap-nests), (b) cardinal direction of trap-nest entrances, (c) maximum height of vegetation within 1 m of the trap-nest, (d) percent pervious surface area within 1 m of the trap-nest, (e) mean light intensity in June, and (f) water index. Methodological details for (c)–(f) are in Table S4. 3. Each datapoint represents 1 trap-nest in a given site and year.

(a) Objective 1



(b) Objective 2

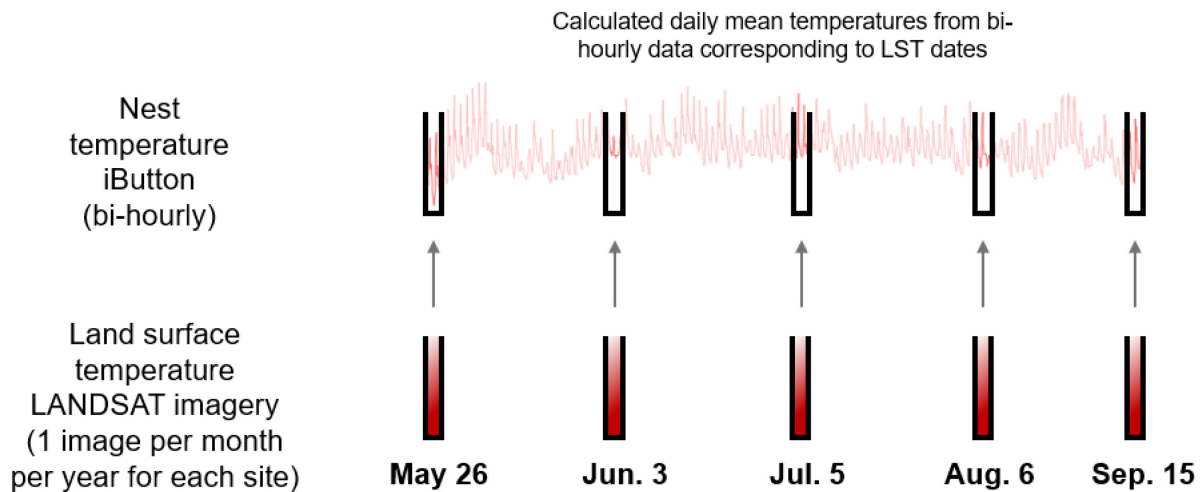


Figure S4. 4. Diagram of temporal windows for temperature predictors.

Temporal windows over which temperature predictors were averaged over in models. There was 1 iButton per trap-nest and multiple trap-nests per site. Temperature was logged every two hours in trap-nests. (a) To test the relationship between nest temperature and juvenile mass we used mean temperature averaged over all iButton records from May 24 to September 17 in each year. (b) To test the relationship between temperature at different spatial scales we calculated daily mean nest temperatures using the iButton data for the specific dates represented by the land surface temperature data which were derived from LANDSAT thermal imagery. Sites were generally represented by 5 values in each year of the study, 1 for every month from May to September.

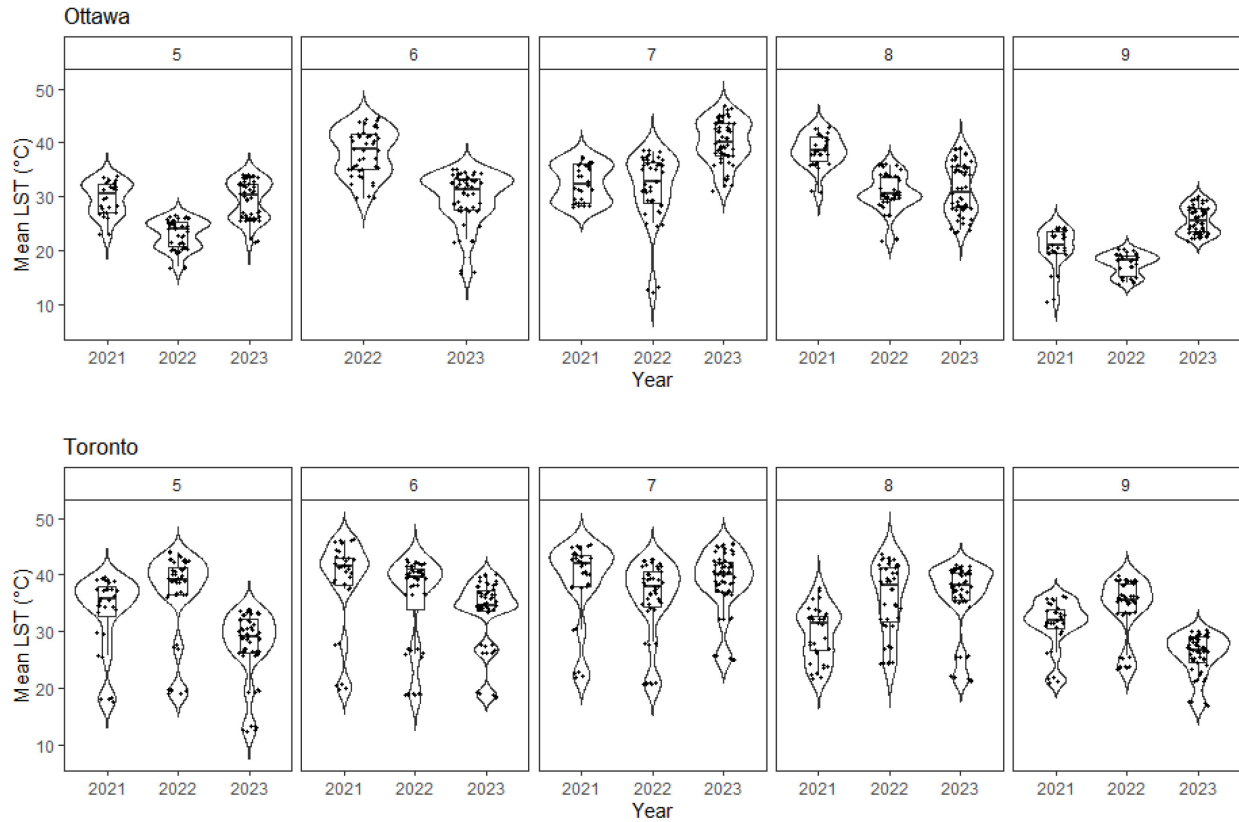


Figure S4. 5. Mean land surface temperatures by year.

Mean land surface temperatures (LST) at 31 sites in Ottawa and Toronto, Ontario over 3 years separated by month (May to September). Each datapoint represents one site in a given month and year (5 datapoints per site per year except for Ottawa sites in 2021; all June thermal images had very high cloud cover). Datapoints were jittered to better visualize data. Box plots indicate temperature ranges over the summer for each year (box = interquartile range, horizontal line within box = median LST, whiskers extending from boxes = minimum and maximum elevations).

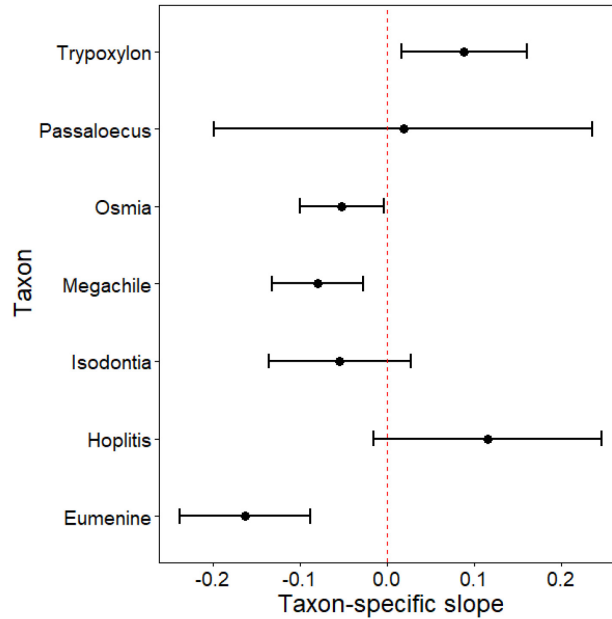


Figure S4. 6. Taxon-specific effects of temperature on juvenile mass.

Taxon-specific random slopes for the effect of mean summer nest temperature on juvenile mass. Note that because taxonomic variation in responses to temperature were considered as a random slope term, the points in the figure represent taxon-specific deviations from the population-level effect (the influence of the population mean is higher for poorly-represented taxa). A linear-mixed effects model was used to generate these slopes because confidence intervals are not available for Gamma GLMMs (which were used to test Objective 1); however, the slope estimates in both the linear and Gamma models were qualitatively identical.

Supplementary references

- Avdan, U. & Jovanovska, G. (2016) Algorithm for Automated Mapping of Land Surface Temperature Using LANDSAT 8 Satellite Data. *Journal of Sensors*, **2016**, 1480307.
- Earth Resources Observation and Science (EROS) Center. (2020). Landsat 8-9 Operational Land Imager / Thermal Infrared Sensor Level-2, Collection 2 [dataset]. U.S. Geological Survey. <https://doi.org/10.5066/P9OGBGM6>.

Esri Inc. *ArcGIS Pro*. Version 2.5. Released February 6, 2020.

Appendix E - Marginal R² values across chapters

Table S0. 1. Explanatory power of climate predictors across chapters (marginal R² values).

Marginal R² values characterizing the univariate relationships between climate variables and total brood cell production (individual reproductive output) for Chapters 1 and 2, and juvenile mass for Chapter 4. Note that multivariate models which included other predictors or covariates were used to examine overall relationships and that these univariate models were used only to evaluate the explanatory power of climate variables. “Average daily accumulated degree-days” represents average conditions experienced by each individual bee over the course of her nesting duration. One degree-hour accumulated whenever the hourly temperature was 1°C above the threshold temperature of 10 °C between 08:00 and 20:00 hr (e.g., an hourly temperature observation of 15 °C equals 5 degree-hours). Models were run separately for each species in Chapter 1. Summer precipitation, temperature, and drought severity for Chapter 2 were calculated as mean temperature conditions from May to August for each site and year. For Chapter 4, summer nest temperature represents mean temperatures inside trap-nests from May 24 to September 17 of each year.

Chapter	Response variable	Predictor	R ² _m	Reference
1	Total brood cell production	Average daily accumulated degree-days	<i>O. iridis</i> : <0.001 <i>O. coloradensis</i> : <0.001 <i>O. montana</i> : 0.08 <i>O. subaustralis</i> : 0.07 <i>H. fulgida</i> : 0.01	Appendix A: Table S1. 6
2	Total brood cell production	Summer precipitation	< 0.01	Appendix B: Table S2. 6 Table S2. 6. R ² values for individual predictors.
		Summer temperature	< 0.01	
		Summer drought severity	< 0.01	
4	Juvenile mass	Summer nest temperature	<0.01	Reported in-text

Appendix F - Miscellaneous natural history observations

This appendix contains a collection of anecdotal observations I made while conducting fieldwork in Colorado for this dissertation (Ch. 1–3). Some of these observations have no direct relation to the thesis, but I include them here for documentation purposes and in case others find them useful for future studies.

Trap-nesting insects from Colorado

Interesting features of the aster-specialist trap-nest occupants

Date:

General observations from 2017–2024

Context:

Observations made while checking trap-nest occupancy at high-elevation sites for Chapter 3 (Avery Peak, Mount Baldy, Gothic Mountain), at Jessica Forrest’s long-term trap-nest monitoring sites (Chapters 1 and 2), and sites in and around the RMBL used for a larval transplant experiment (not included in this thesis).

Observations:

Osmia montana and *Osmia subaustralis* (both in the subgenus *Cephalosmia*) were frequently observed trap-nest occupants in our study area. Females of both species provision their nests exclusively with aster pollen, both use masticated leaf material to construct brood cell walls, and both pack their brood cells very tightly with pollen, leaving little to no space between the pollen provision and nest walls. (As an aside, the pollen provisions are crumbly in texture, and have a sweet, yeasty, slightly fermented taste and odour).

They are similar in body size; however, in bright sunlight, females of *O. subaustralis* seemed to have a slightly bluer and more iridescent integument with lighter-coloured hairs compared to *O. montana*, whose integuments appeared darker and had black hairs (Figure S0. 1a & b). A front view of the females of these species allowed them to be easily distinguished as *O. montana* females have much larger jaws compared to *O. subaustralis*.

In Chapter 3, I combined data for these two species in analysis, noting that their nests were morphologically indistinguishable. (I was also unable to ascertain the identity of the nest occupant based on the distinguishing morphological features of the nesting females as nests were not monitored sufficiently frequently). That said, I did notice some differences in nest construction (which did not manifest consistently enough for me to rely on them). Namely, the construction habits of *Osmia subaustralis* seemed less tidy compared to those of *O. montana*. For the former, I often observed crumbs of pollen conspicuously scattered around the nest entrance (Figure S0. 1c) and smeared on the wood of the trap-nest near the entrance. These residues typically remained even after the nest was completed and sealed. The occupant herself (if seen) also often had pollen residues clinging to the hair on her face. In contrast, *O. montana* nests were generally more kempt. There were sometimes stray crumbs of pollen inside the nest during its active construction, but these were usually tidied up by the nest owner. I noted however, that *O. montana* nests sometimes had a pale, and barely distinguishable yellow stain along the inside of the unoccupied portions of the nest (Figure S0. 1b). Perhaps this stain was produced by the occupant tidying the crumbs of pollen by dragging them along the straw.

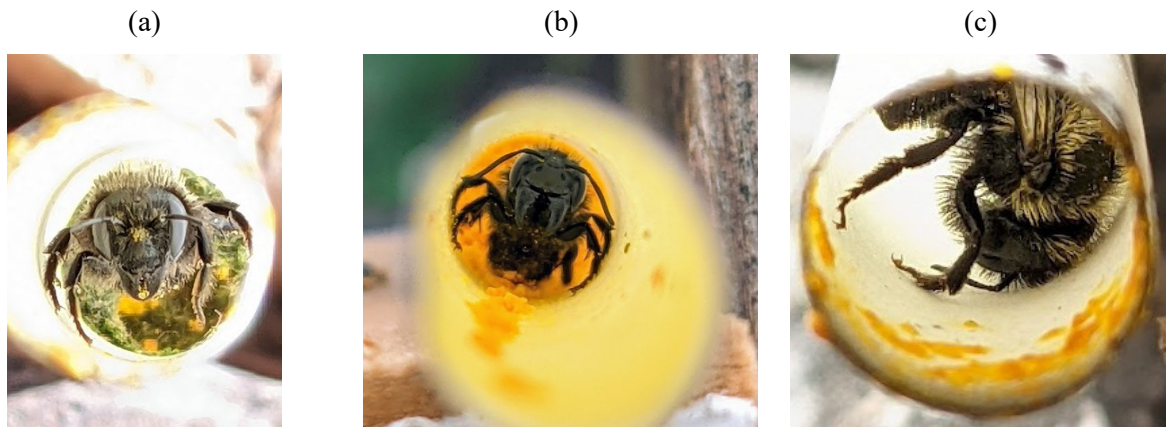


Figure S0. 1. Distinguishing features of cavity-nesting aster specialist bees.

(a) *Osmia subaustralis* females have smaller jaws and lighter-coloured hairs. (b) *Osmia montana* females have large jaws and darker integument and hair. There is a pale, yellow stain along the unoccupied portion of the straw, and some stray pollen crumbs that were likely tidied up before this individual sealed her nest (although I unfortunately neglected to make note of whether this was the case for this particular nest). (c) Pollen crumbs are present around the nest entrance of this *O. subaustralis* individual (who happened to have been in the process of re-orienting herself in the nest when this photo was taken). Photo credit: LHW.

Differences in nest construction aside, I also noted that *Osmia subaustralis* females seemed bolder—if the nesting female happened to be present when I extracted the paper straw containing her nest, she often ran

towards the nest entrance in a seemingly defensive way, even moving backwards and forwards repeatedly as if charging. In the same situation, *O. montana* females generally withdrew to the back of their nests.

Notes on aster specialist occurrences:

Osmia coloradensis was the third aster specialist often observed in the trap-nests in this area. Nesting females and their nests were easily distinguished from the other two aster specialists. Females of this species used small-sized straws almost exclusively, generally had earlier phenology, had a slenderer body, and very distinct faces with more hair. They also left a small gap between the pollen provision and nest walls. *Osmia coloradensis* were frequent occupants of trap-nests at Brush Creek and Rosy Point (the two lowest elevation sites among Jessica Forrest's long-term sites; see Table S2. 1). This species was never observed at Virginia Basin throughout the entire duration of the study period (2013–2023).

Osmia subaustralis seemed to be more strongly associated with cooler sites. They were observed consistently at sites beyond treeline for Chapter 3 and were the most common occupants of trap-nests at Virginia Basin and Kebler Clearing (the two highest and coolest sites among Jessica Forrest's long-term sites; see Table S2. 1). They were rarely observed at the lowest elevation site at Brush Creek; the only year they were observed at this site was in 2019, which was a particularly cool year characterized by high winter precipitation such that the site at Virginia Basin did not melt out until the end of June. In the long-term data, *Osmia montana* occurred most frequently at Rosy Point (lower elevation, warmer) but also occurred frequently at sites of intermediate elevation among Jessica Forrest's long-term sites (e.g., Kebler Clearing and 401 Trail), and occasionally at Virginia Basin. I note here that for Chapter 3, I only ascertained *O. montana* nesting activity (i.e., I saw the nesting female) at the Avery Peak sites; this species was never observed in trap-nests at sites along Mount Baldy or along West Gothic. All nests recorded as "*Cephalosmia*" at the later two mountains were therefore most likely *O. subaustralis* nests. It would be interesting to further investigate these species-specific climate associations.

***Hylaeus* "barricaded" in by another trap-nest occupant**

Date:

July 24, 2023

Context: Checking trap-nest occupancy at high-elevation sites (Avery Peak).

Observation:

I found a female *Hylaeus* locked in the back of an *O. subaustralis* nest which was in progress. The latter must have constructed a rear wall while the former was sitting in the back of the straw. I cut a window in the back “cell” to free the *Hylaeus*.

Mistaking *Potentilla* for an aster

Date:

2023

Context:

Checking trap-nest occupancy at high-elevation sites (Avery Peak)

Observations:

On one occasion, when the *Potentilla* shrubs had recently come into bloom, I witnessed an *Osmia subaustralis* female exit her nest and fly straight towards an open *Potentilla* flower from a shrub less than 30 cm away from the nest. She landed on the flower, circled over the center of it several times as if rummaging for pollen before departing. I wonder if she momentarily mistook the *Potentilla* flower for an aster. To a human observer, *Potentilla* is similar in symmetry and colour to many asters. Later that day, I observed an *Osmia subaustralis* female (possibly the same individual) removing pulp from the leaves of the same plant, presumably for wall material.

***Passaloecus* (aphid wasps)**

Date:

2023

Context:

Checking trap-nest occupancy at high-elevation sites (Avery Peak)

Observations:

Solitary wasps in the genus *Passaloecus* provision their nests exclusively with aphid prey (Iwata 1976). They were occasionally observed at Jessica Forrest’s sites (including Virginia Basin), but among the wasp occupants, they were not as commonly observed as the Eumeninae spp. Over the three years of the study, I observed three *Passaloecus* nests at the high-elevation sites, all in 2023. The resin they use as wall material is exceptionally sticky—an attempt to extract the straw left the prongs of my forceps very sticky. It is a wonder as to how they avoid getting the substance on their wings and legs when coming and going

from their nests which often have a ring of resin at the entrance while it is still active. Of the three *Passaloecus* nests I observed at the Avery peak sites, two contained only resin and no aphids. There were spruce krummholz trees around (perhaps the source of the resin), but I did not come across any aphid colonies in my ramblings around those sites, even though *Ligusticum porteri*—a plant that is often coated with aphids at lower elevations—was highly abundant at many of the sites. It would be interesting to learn about the extent to which the distributional limits of these wasps are constrained by the availability of their prey. Their rarity in trap-nests (even at low elevations) could however be partly due to their preference for nest cavities that are smaller in diameter than those in our trap-nests as females are very small-bodied compared to most other taxa observed occupying trap-nests.

Juvenile development at high elevations

Date:

2022–2023

Context:

Checking trap-nest occupancy at high-elevation sites for Chapter 3

Observations:

The highest-elevation site among those used for Chapter 3 was 3700 m, near the summit of Gothic Mountain. In 2022, two cavities in the trap-nests at this site were occupied by *Hoplitis* spp. (at least one of which was *H. fulgida*) containing 8 and 2 brood cells respectively. The nests may have belonged to the same individual. When I examined the contents of these two nests at the end of the field season that year (late July 2022), I noted that the pollen provisions were uneaten in most of the cells. When I inspected the cells with uneaten pollen, some had a small divot in the provision which may have been where an egg once laid but was no longer. In two of the ten cells (1 in each nest), I saw that the developing individual had successfully spun a cocoon. I left both nests in place over winter and moved them to a new “emergence” trap-nest for the following summer (2023). By mid-August of 2023, I noticed that the outer seal was still intact for both nests. I inspected their contents. One of the cells had completely succumbed to mold and water damage. The other had a live *H. fulgida* individual still in his cocoon case. He crawled out from an opening I made in his cocoon, and I noticed that he did not yet have fully-formed wings. Although females may be able to provision nests at these high elevations, I wonder if the growing season is still too cool and/or brief for their offspring to successfully complete development.

Cocoon material

Date:

General observations from 2021–2024

Context:

Checking offspring success from larval transplant experiment (not included in thesis)

Observations:

The cocoon material of all *Osmia* (primarily *O. iridis*, but also *O. coloradensis*) is much more durable compared to that of *Hoplitis fulgida*. *Osmia* cocoons are stretchy and difficult to tear. They also seem less likely to let mold penetrate. *Hoplitis* cocoons were thin, translucent, papery in texture, and brittle. They sometimes cracked or tore upon handling, and the developing larva is sometimes visible through the cocoon fibres.

Kleptoparasitism

Date:

2021–2023

Context:

Checking trap-nest occupancy at high-elevation sites for Chapter 3

Observation:

Kleptoparasitic wasps in the family Sapygidae were commonly observed at Jessica Forrest's long-term sites, the most abundant of which was a species in the genus *Sapyga* which were parasites of *Osmia iridis* (Forrest and Chisholm 2017). A species in the genus *Krombeinopyga* was also observed parasitizing nests of *Hoplitis* spp. While collecting data for Chapter 3, I observed sapygid wasps flying around trap-nests at the three lower sites along the slope of Avery peak (3450 m–3500 m), but not at sites beyond those. Since I did not observe *Osmia iridis* nesting in the trap-nests for Chapter 3 (but see observation entry below), and these kleptoparasites seem to avoid attacking the nests of aster specialists (Spear et al. 2016), I presume that their only potential hosts would have been the nests *Hoplitis* spp. or perhaps of *O. tristella*. I cannot confirm that parasite attack actually occurred as I only observed sapygids frequenting the trap-nest area but did not inspect each brood cell for parasite eggs or larvae for this project. I also note that I did not observe sapygid activity at Mount Baldy or at Gothic Mountain. I did observe the kleptoparasitic bee *Stelis* spp. on three occasions during insect surveys (once on the third and fifth Avery site (3500 m and

3600 m respectively), and once on the third Baldy site (3500 m))

<https://www.inaturalist.org/observations/88129554> and

<https://www.inaturalist.org/observations/128388379>.

***Osmia iridis* beyond treeline?**

Date:

June 23, 2023, and July 1, 2023

Context:

Checking trap-nest occupancy at high-elevation sites for Chapter 3 at Avery Peak site 2

Observation:

The pollen provisions of the nests of *Osmia iridis* contain only pollen from plants in the legume tribe *Fabeae*. Despite high abundances of this species in the trap-nests at most of Jessica Forrest's long-term sites (see Chapters 1 and 2), this species was rarely observed occupying trap-nests at the highest elevation site at Virginia Basin (only 5 individuals recorded throughout the duration of the study; compared with 107 individuals at Rosy Point). The absence of their host-plants was likely not the reason for their rarity at Virginia Basin as both *L. lanszwertii* and *V. americana* were present. These plants also occurred in similar abundances at the sites used for Chapter 3. In the entry above, I noted that I did not observe *Osmia iridis* nesting in the high-elevation trap-nests used for Chapter 3; however, I suspect that one nest I observed at the second Avery site in 2023 (340 m) may have belonged to an individual of this species. This nest was the first nesting activity recorded for that field season at these sites and was observed during a period of particularly high *L. lanszwertii* abundance. The construction of the nest seemed characteristic of the *Osmia iridis* nests I had observed at lower elevations: the provision was orange-coloured and liquid-y and when I examined its contents under a microscope from a sample, it contained only Fabaceae pollen. I never saw the nesting female, and the nest was abandoned with no seal after only partial completion of the third cell (approximately 2.7 brood cells in total).

Other high-elevation animals

The following are miscellaneous notes unrelated to trap-nest occupants from the high-elevation sites used for Chapter 3 (and the peaks above them):

June 15, 2024: I observed a male *Osmia* on *Smelowskia americana* near the summit of Gothic Mountain which is approximately 150 m higher in elevation than my highest site for this chapter (highest site = ~3700 m, Gothic summit = 3850 m). There was no woody material for long distance from here, only loose scree and talus. Perhaps this is a hill-topping male? Photo submitted to iNaturalist:

<https://www.inaturalist.org/observations/223687632>

July 15, 2023: I observed a male *Agapostemon* on *Senecio* during insect surveys at the fourth Baldy site (3550 m). <https://www.inaturalist.org/observations/182050386> I have not seen one so high before. From a quick GBIF examination (March 2026), there are no sightings of *Agapostemon* spp. above 2450 m in Western North America (West of Nebraska). Dr. Rebecca Irwin's data suggest there have been a handful of observations of *Agapostemon texanus* at sites around 3000 m.

2021–2022: A ground-dwelling bird (Phasianidae spp.) was present in the patch of *Mertensia ciliata* about 30 m from the site centre of the second Baldy site (3475 m) for two years. I did not see this individual in 2023. I was never able to see her closely as she always flushed suddenly when I drew near (and I was consistently startled by this).

2021–2023: The pollen-collecting wasps *Pseudomasaris marginalis* and *Pseudomasaris zonalis* which forage primarily from *Phacelia* species were observed 14 times over the three years of insect surveys. *Phacelia hastata* and *Phacelia sericea* occurred at 8 out of the 14 sites at which I conducted surveys. *Pseudomasaris* spp. were observed at 1 out of the 3 sites where *Phacelia* occurred at Avery, and 4 out of the 5 sites where this plant occurred at Baldy, including the highest-elevation site (3675 m)

https://www.inaturalist.org/observations?taxon_id=211886&user_id=lydiaahagarwong&verifiable=any

2022–2023: A lactating female golden mantled squirrel (*Callospermophilus lateralis*) frequented the fifth Avery site in 2022 and 2023 (~3600 m; <https://www.inaturalist.org/observations/128386861>). She seemed unbothered by my presence and often helped herself to exploring the contents of my gear.

2022–2023: A single marmot frequented the seventh Baldy site in both years (~3650 m; <https://www.inaturalist.org/observations/128347683>). This individual was similarly unbothered by my presence and assumed the habit of gnawing on the cork of my trekking poles if I left them unsupervised.

*Solitude is only a human presumption. Every
quiet step is thunder to beetle life underfoot;
every choice is a world made new for the
chosen. All secrets are witnessed.*

~ Barbara Kingsolver, *Prodigal Summer*