THESIS

FROM SOIL TO AIR: EXPLORING TWO NOVEL APPROACHES TO STUDYING CRYPTIC ASPECTS OF INSECT ECOLOGY

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Sophia Maria Gulutzo

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Master's Committee:

Advisor: John M. Mola

Ian Pearse

Liba Pejchar

ABSTRACT

FROM SOIL TO AIR: EXPLORING TWO NOVEL APPROACHES TO STUDYING CRYPTIC ASPECTS OF INSECT ECOLOGY

Insects play critical roles in forest ecosystems; however, their overwintering ecology and spatial behavior remain poorly understood due to methodological challenges in observing their cryptic life stages and movements. This thesis integrates two complementary approaches to address these gaps in montane forests of Colorado. First, we used soil emergence traps to investigate how fine-scale microhabitat conditions—including canopy cover, duff depth, basal area, and ground cover—affect spring insect abundance and emergence phenology. Across 77 traps, we recorded 1,286 insects, dominated by Coleoptera, Hymenoptera, and Hemiptera. Although patterns of abundance and emergence timing were highly variable, no environmental predictors showed statistically significant effects, suggesting that unmeasured microclimatic factors and species-specific traits likely drive overwintering outcomes. Second, we evaluated the feasibility of applying very high frequency (VHF) radio telemetry to bumble bees (*Bombus* spp.), testing morphological predictors of flight success in mock-tag trials and conducting field deployments with Lotek NanoPin transmitters. Body mass emerged as the dominant determinant of flight ability, with a threshold of ~310 mg required for even-odds flight, a size exceeded primarily by queens and large workers. Field trials revealed limited relocation success, with signals often lost within minutes to hours, underscoring the influence of terrain, vegetation, and receiver strategy on detection. Together, these studies highlight both the promise and constraints of emerging methods for studying cryptic phases of insect ecology. Soil emergence traps provide community-level insight into overwintering dynamics, while telemetry—though currently constrained by body size and signal range—offers potential for directly locating nests and tracking movement. By pairing habitat-based and individual-based approaches, this work advances understanding of insect persistence and phenology in montane forests and establishes methodological baselines to inform future research under changing climatic conditions.

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CHAPTER 1: LINKING MONTANE MICROHABITATS TO OVERWINTERING INSECT ABUNDANCE AND PHENOLOGY USING SOIL INSECT EMERGENCE

1.1 Introduction

Montane forests present a challenging winter environment in which insects must survive prolonged subfreezing temperatures and deep snow cover. Overwintering is often a critical bottleneck for insect populations, limiting species distributions and regulating year-to-year abundances in these high-elevation ecosystems (Bale & Hayward 2010; Marshall et al. 2020). Many montane insects have a univoltine life cycle with an extended dormant period, ensuring that the most cold-vulnerable life stages are sheltered during the harsh winter months (Danks 2002; Williams et al. 2015). Insects have evolved a suite of behavioral and physiological adaptations to endure the rigors of winter. Understanding these strategies in montane forest species is key to predicting their persistence and responses to climate change (Bale 2002; Sinclair et al. 2015).

Climate change is rapidly altering overwintering conditions in temperate and montane ecosystems by reducing snowpack, increasing winter temperature variability, and amplifying freeze–thaw cycles (Cooper 2014; Williams et al. 2015). These shifts threaten to disrupt overwinter survival and the timing of spring emergence, particularly for insects with narrow thermal thresholds or rigid phenological schedules (Sinclair et al. 2015). Because overwintering strategies are shaped not only by physiology but also by the buffering effects of microhabitats, understanding how fine-scale habitat conditions influence emergence is increasingly important in the context of changing winter regimes (Sinclair et al. 2003; Bale & Hayward 2010).

A central adaptation for winter survival in insects is the development of cold hardiness, which enables individuals to withstand subfreezing temperatures (Bale & Hayward 2010). Many species enter diapause in response to environmental cues such as photoperiod and temperature and adopt either freeze-tolerant or freeze-avoidant strategies to survive overwintering conditions (Leather et al. 1993; Sinclair et al. 2002). Although these physiological mechanisms are well-documented in laboratory settings, their expression in natural habitats is shaped by microclimatic variation and remains less well studied in field contexts (Sinclair et al. 2002; Bale & Hayward 2010).

Insects overwinter in a wide variety of microhabitats (Niemelä et al. 1996), including beneath bark, within rotting logs, under stones, in soil, and beneath leaf litter (Leather et al. 1993; Bale & Hayward 2010). These environments buffer against extreme temperatures, reduce the risk of desiccation, and provide protection from predators (Sinclair et al. 2003; Bale & Hayward 2010). Snowpack can offer additional insulation, particularly in montane ecosystems, where it helps moderate freeze–thaw cycles and maintains stable subnivean temperatures (Leather et al. 1993; Bale & Hayward 2010). Microhabitat selection is often species-specific and influenced by life stage, resource availability, and environmental conditions. However, field-based data on overwintering site use remain limited for many insect groups, especially in relation to environmental gradients in forested ecosystems.

Despite the ecological importance of insect overwintering, it remains difficult to study directly due to the cryptic and inactive nature of most species during colder months (Leather et al. 1993). Traditional survey techniques such as pitfall trapping or mark–recapture are often ineffective during winter, especially in snow-covered or frozen habitats. As a result, much of our understanding of overwintering ecology comes from laboratory studies of cold tolerance and diapause physiology (Sinclair et al. 2003; Bale & Hayward 2010), which may not fully capture the influence of natural habitat variability. Emergence traps (Figure 1) offer a practical field-based alternative, allowing researchers to monitor insects as they exit overwintering sites in spring.

Figure 1. Photo of a BugDorm Soil Insect Emergence Trap (Model BT2013) deployed on the forest floor.

In this study, we investigated how fine-scale environmental conditions influence insect emergence timing and abundance in upper montane lodgepole pine forests. We hypothesized that traps located in more insulated microhabitats - characterized by deeper duff, greater canopy cover, and higher basal area—would exhibit greater insect abundance and later peak emergence. Although emergence traps have been widely used in agricultural and forest settings, few studies have linked emergence patterns to local-scale environmental variability across heterogeneous forest landscapes. By pairing trap-based sampling with environmental measurements, this study aims to clarify how microsite conditions shape spring insect emergence, providing field-based insight into overwintering outcomes and phenological shifts in montane forest systems.

1.2 Materials and Methods

1.2.1 Study Area and Design

Our study was conducted in the southern Rocky Mountains near Colorado State University's Mountain Campus, near Bellvue, Colorado (40.7680 N, 105.7747 W). The region is characterized by upper montane forests, primarily composed of lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and mixed conifer communities (Kaufmann et al. 2006). The study area has experienced recent wildfire disturbance, notably from the High Park Fire in 2012 and the Cameron Peak fire in 2020. These disturbances created a heterogeneous mosaic of canopy cover and ground conditions across the landscape.

Because our primary goal was to quantify how local microhabitat features influence insect emergence and abundance, we deployed soil emergence traps across a gradient of canopy cover and ground conditions at four lodgepole pine forest sites. Each trap served as the unit of replication in our analyses, enabling us to examine fine-scale habitat effects on emergence patterns. Due to accessibility limitations, sites were chosen opportunistically at locations approved by CSU Mountain Campus and partners with the US Forest Service. Site was treated as a random effect in statistical models to account for unmeasured environmental variability and to capture potential clustering among traps placed at the same site.

1.2.2 Trap Setup

To sample emerging insects from the soil, we deployed 20 BugDorm Soil Insect Emergence Traps (model BT2013; Megaview Science Co., Ltd., Taiwan) at each site. Each trap consists of a pyramid-shaped mesh tent with an attached collecting bottle at the apex (Figure 1). Emerging insects move upward through the mesh towards the top of the trap and are captured in the bottle, which was partially filled with a 1:1 ratio of propylene glycol and water.

We placed traps directly on the ground surface. The trap side flaps were buried under the surrounding substrate to minimize insect escape. Trap locations were placed semi-randomly in a rough transect intended to capture a visually estimated gradient of canopy cover at each site. Traps were monitored weekly for 10 weeks, from May 1 to June 30, 2024. During each visit, the integrity of the traps was checked, and insect specimens were collected by straining the collection vial contents through a mesh funnel and transferring the specimens into a vial containing 80% ethanol. If a trap was disturbed or compromised (e.g., by wildlife), it was removed from further sampling without replacement.

1.2.3 Field Data Collection

At each trap location, we recorded multiple environmental variables to characterize local habitat conditions. Canopy cover (%) was measured using a spherical densiometer (Forestry Suppliers, Jackson, MS). Four measurements (one in each cardinal direction) were averaged to estimate percent canopy cover. Microhabitat composition was recorded as the dominant ground cover at each trap. Categories of dominant land cover included bare ground, conifer needle litter, hardwood leaf litter, coarse woody debris, grass, forbs, or shrubs. Tree basal area (ft2/acre) was estimated using a Cruz-all Timber Cruiser (factor 5). Trees that fully fit within the viewing window were tallied, and the count was multiplied by five to calculate basal area. To measure duff depth (cm) we took the mean of four measurements, one each taken at each trap corner. All insects were sorted and identified to the taxonomic level of order and counted to determine abundance. Specimens were stored in ethanol for further verification. We excluded Diptera from analyses because these specimens were often very small and numerous, and we were uncertain whether they consistently emerged from within the traps or entered the collection vials opportunistically (e.g., as flying by-catch).

1.2.4 Data Processing and Analysis

All statistical analyses were conducted using R version 4.4.1 (R Core Team 2024). Prior to modeling, raw insect abundance data were inspected for outliers and potential misidentifications. Continuous variables (canopy cover, basal area, and duff depth) were standardized (z-transformed) to improve model interpretability and convergence.

To assess overall insect abundance across traps, we fit a Generalized Linear Mixed Model

(GLMM) with a negative binomial error structure using the glmer.nb() function in the lme4 package (Bates et al. 2015). Fixed effects included standardized canopy cover, duff depth, basal area, and dominant microsite type. Site was included as a random intercept to account for spatial non-independence of traps. Model dispersion was assessed, and the negative binomial distribution was selected to correct for overdispersion relative to a Poisson model. We then repeated this same procedure for each of the top three represented insect orders (Coleoptera, Hymenoptera, and Hemiptera) separately to look at the effects of canopy attributes and microsite characteristics on these orders specifically.

To investigate environmental predictors of the timing of peak emergence, we identified the collection date with the maximum recorded insect abundance for each trap. We then fit a Linear Mixed-Effects Model (LMM) using the lmer() function to model the day of year (DOY) of peak emergence as a function of the same above measured predictor variables (canopy cover, duff depth, basal area, and dominant microsite type) and with site as a random effect.

1.3 Results

1.3.1 Total insect abundance

Across 510 trap collections from 77 traps (3 were removed and excluded due to disturbance by wildlife), we recorded a total of 1,286 insects (excluding Diptera). The highest single-trap abundance was 39 individuals, and overall emergence activity peaked around June 19, 2024. The most represented orders were Coleoptera (598 individuals), Hymenoptera (252), and Hemiptera (219), followed by Orthoptera (110), Lepidoptera (101), Neuroptera (4), and Odonata (2). When modeling total insect emergence, none of the fixed effects—canopy cover, duff depth, basal area, or dominant microsite type—were statistically significant (all $p > 0.1$), although estimated coefficients for basal area and certain microsite categories exhibited positive trends (Figure 2). The random effect of site accounted for minimal variance (0.021), suggesting most variability occurred at the trap level rather than among sites.

In terms of dominant microsite type, traps placed over coarse woody debris and leaf litter tended to have slightly higher insect abundance, while those on bare ground and shrub cover had lower values; however, these patterns were not statistically significant (Figure 2D). Grass, forbs, and shrubs were not dominant groundcover at any trap, so they were excluded from our analyses.

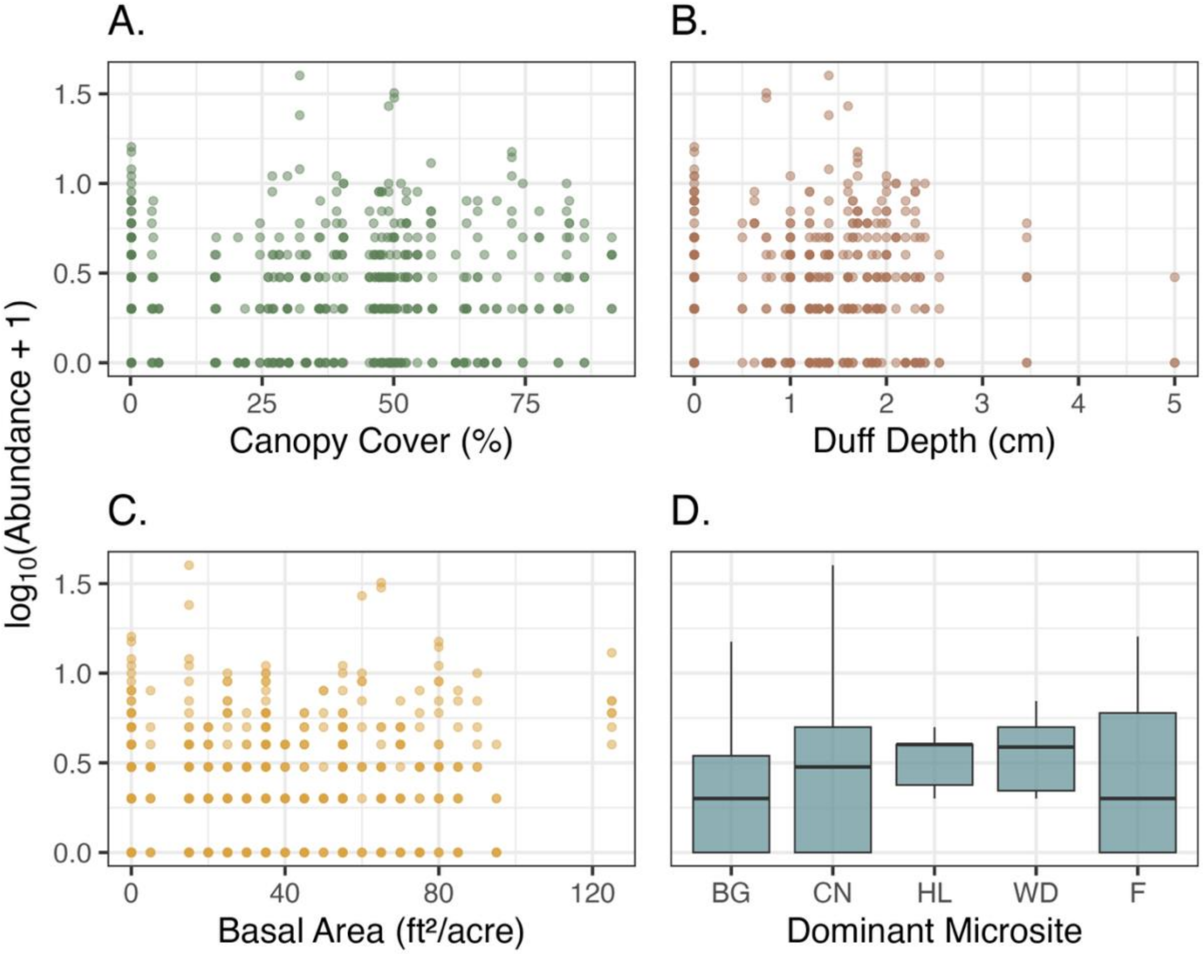

Figure 2. Relationships between total insect abundance ($\log_{10}$-transformed) and environmental predictors across 510 trap-day observations. Points represent trap-level data. Trend lines with 95% confidence intervals are shown for continuous variables. (A) Canopy cover (%), (B) duff depth (cm), and (C) basal area (ft²/acre) show weak positive trends. (D) Abundance by dominant microsite type; no statistically significant differences were observed. X-axis key: BG = bare ground, CN = conifer needle litter, HL = hardwood leaf litter, WD = woody debris, F = forb.

1.3.2 Peak emergence timing

A linear mixed-effects model (LMM) was used to assess environmental predictors of peak emergence timing, measured as the day of year (DOY) with the highest insect abundance per trap (n = 77). No environmental predictors were statistically significant (Figure 3). Duff depth showed a marginally negative trend (estimate = –2.91), suggesting earlier emergence in traps with deeper duff layers. Dominant microsite type did not significantly affect peak timing, though traps on woody debris and hardwood litter showed slightly later median emergence dates compared to other microsites (Figure 3D).

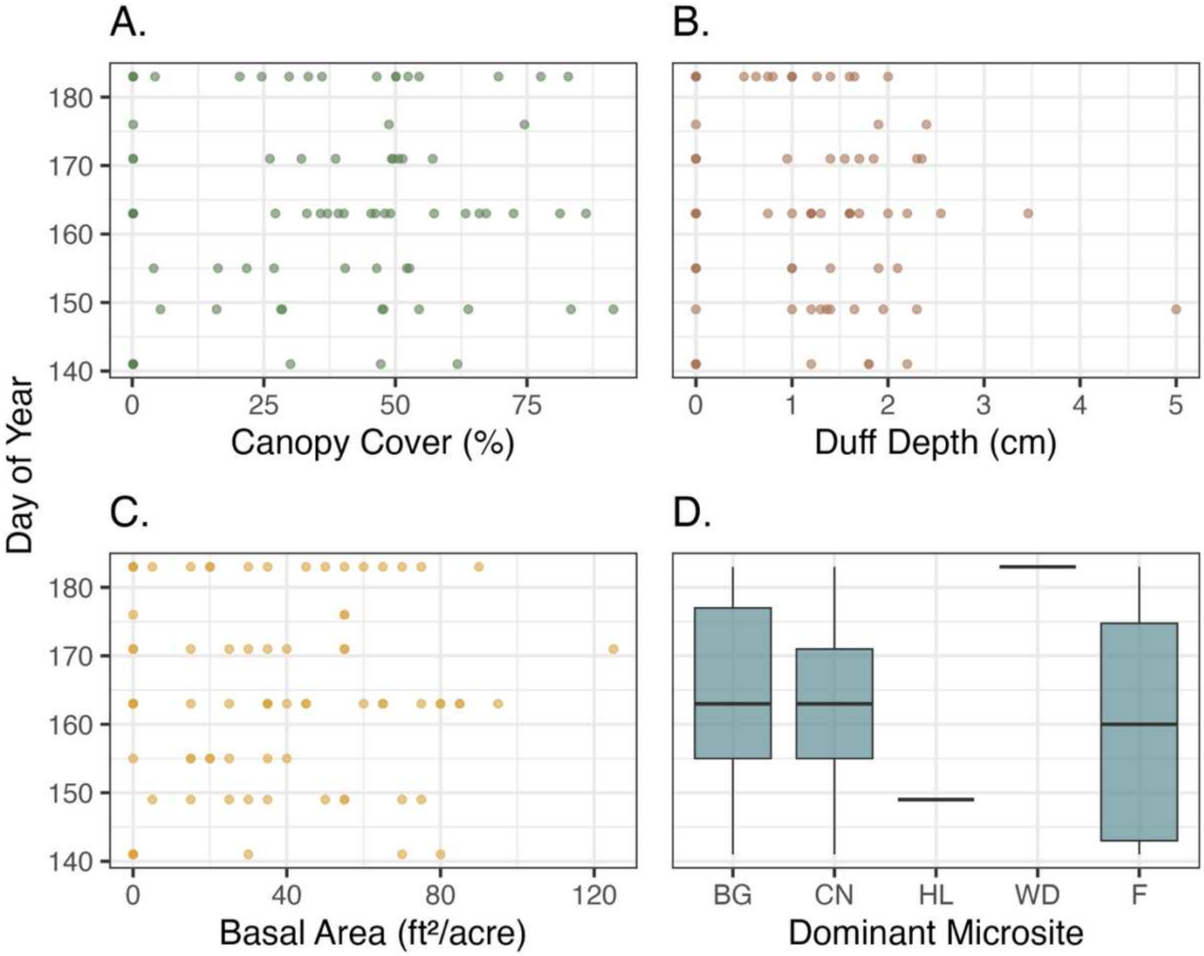

Figure 3. Effects of canopy cover, duff depth, tree basal area, and microsite type on the seasonality (day of year) of peak insect emergence for 77 traps. (A) Canopy cover, (B) duff depth, and (C) basal area showed weak associations with peak timing; deeper duff layers were associated with slightly earlier emergence (estimate = –2.91), though not statistically significant. (D) Peak DOY by dominant microsite type; traps over woody debris and leaf litter had later median emergence dates, though variation was high and differences were not significant. X-axis key: BG = bare ground, CN = conifer needle litter, HL = hardwood leaf litter, WD = woody debris, F = forb.

1.3.3 Order-level analyses

Separate LMMs were fit for the three most abundant orders (Figure 4). For Coleoptera, no environmental predictors were significant, although slight positive trends were observed with canopy cover and basal area. For Hymenoptera, duff depth had a relatively stronger negative effect (estimate = –2.68), suggesting earlier emergence in deeper duff. Hemiptera abundance appeared most variable, showing higher site-level structuring and a positive (though non-significant) trend with canopy cover (estimate = 4.26). Microsite effects were generally weak across orders; however, Hemiptera displayed greater variation among microsite types, with highest median abundance in traps over hardwood leaf litter and coarse woody debris (Figure 4D).

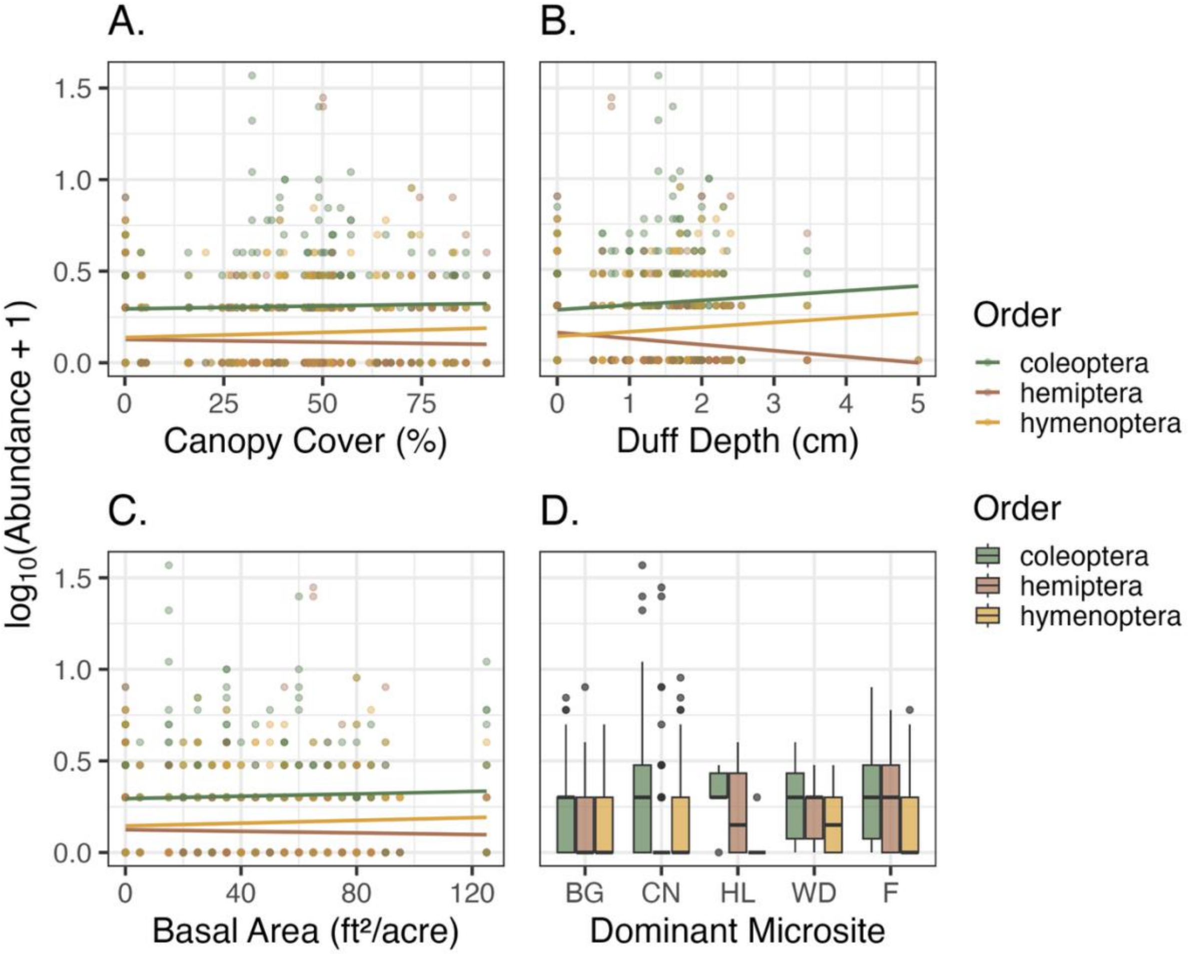

Figure 4. Abundance patterns for the three most abundant orders (Coleoptera, Hymenoptera, Hemiptera), $\log_{10}$-transformed. Points represent individual trap collections. (A) Abundance vs. canopy cover, (B) abundance vs. duff depth, (C) abundance by canopy cover, and (D) abundance by dominant microsite. No statistically significant trends were detected; however, Hemiptera abundance showed greater variation among microsite types, particularly with higher abundance over hardwood litter and woody debris. X-axis key: BG = bare ground, CN = conifer needle litter, HL = hardwood leaf litter, WD = woody debris, F = forb.

1.4 Discussion

To understand how insects persist through harsh montane winters and how their phenology may shift under climate change, we must examine the role of fine-scale structural and microhabitat features in shaping overwintering success. To address this gap, we quantified insect emergence patterns in relation to duff depth, canopy cover, and basal area using soil emergence traps. Therefore, this study assessed how structural and microhabitat features influence the overwinter emergence of soil-dwelling insects in a montane forest ecosystem. Despite expectations that insulated microhabitats (e.g., deep duff or dense canopy) would support higher emergence and delay phenology (Sinclair et al. 2003; Bale & Hayward 2010), we found no statistically significant relationships between environmental predictors and either total insect abundance or peak emergence timing. Our traps yielded a total of 1,286 insects, dominated by Coleoptera (46.5%), Hymenoptera (19.6%), and Hemiptera (17%), yet the patterns of abundance and emergence timing were highly variable across traps. These findings suggest that overwintering success and phenological timing in this system are shaped by a complex array of factors, many of which remain unmeasured or difficult to capture using trap-based methods alone (Leather et al. 2008; Sinclair et al. 2015).

The order-specific models revealed subtle differences among groups. Coleoptera and Hymenoptera showed relatively uniform emergence patterns, whereas Hemiptera displayed greater site-level structuring and more pronounced variation among microsite types. These differences may reflect divergent overwintering strategies, such as variation in diapause intensity or microhabitat preference (Sinclair et al. 2001; Williams et al. 2015). For example, Hemiptera are known to exhibit plastic responses to early spring conditions, potentially contributing to their higher variability (Leather et al. 1993). Future studies could explore whether species-level traits, such as freeze tolerance or microhabitat fidelity, predict these differences more effectively.

Most of the variation in insect abundance and phenology remained unexplained by our models. The lack of strong microsite effects contrasts with studies that suggest forest floor microhabitat features—such as duff depth or woody debris—provide important thermal buffering and shelter (Danks 2002; Sinclair et al. 2015). The exclusion of temperature data due to logger failure likely limited our ability to capture fine-scale thermal variation, a known determinant of overwintering success (Bale & Hayward 2010). Moreover, our estimate of emergence timing based on peak abundance may oversimplify more gradual or multi-modal emergence patterns (Leather et al. 2008).

These limitations take on added significance when considered in the context of ongoing climate change, which is rapidly reshaping winter conditions for montane insects. A well-documented example is the mountain pine beetle (*Dendroctonus ponderosae*), where warmer winters have contributed to increased overwinter survival and altered emergence phenology, amplifying ecological impacts and causing widespread tree mortality across western North America (Safranyik & Carroll 2010; Bentz et al. 2010). However, for many insect taxa, particularly less-studied groups such as non-pest forest floor communities, the interactive effects of winter conditions and microhabitat characteristics remain poorly understood. Our results, showing high variability and largely unexplained emergence patterns despite clear contrasts in microsite conditions, underscore this knowledge gap and highlight the difficulty of predicting community-level responses to winter climate change based solely on coarse habitat metrics.

Taken together, our findings underscore the importance of moving beyond broad habitat proxies to integrated approaches that combine direct microclimate measurements, species-level or trait-based data, and landscape context. As climate change continues to reshape winter regimes, such detailed, mechanistic studies will become increasingly critical for understanding and forecasting insect community dynamics in montane ecosystems.

1.5 Conclusion

The high variability and apparent idiosyncrasy of emergence patterns observed here emphasize the need for continued field-based research on overwintering ecology. Incorporating soil temperature loggers and winter snowpack depth measurements would allow for direct assessment of thermal conditions and buffering capacity at microsites, overcoming one of the major limitations of this study (Bale & Hayward 2010; Danks 2002). Extending sampling windows both earlier in spring and later into summer could help capture gradual or multi-modal emergence patterns that may be missed when using peak-based timing alone. Additionally, identifying insects to species or functional group level would enable detection of trait-mediated or taxon-specific responses to microhabitat gradients. As climate change reshapes montane winters, refining our understanding of how insects interact with fine-scale habitat features and microclimatic variability will be vital for predicting community resilience and forest ecosystem health.

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CHAPTER 2 – EXPLORING RADIO TELEMETRY TO STUDY BUMBLE BEES (*BOMBUS* SPP.) MOVEMENT AND NESTING ECOLOGY

2.1 Introduction

Radio telemetry has emerged and evolved as a transformative tool in wildlife biology since the mid-20th century. The earliest applications in the 1950s and 1960s used large, bulky transmitters to follow mammals and birds, providing the first continuous records of animal space use (LeMunyan et al. 1959; Cochran & Lord 1963; Kenward 2001). Subsequent improvements in battery life, transmitter miniaturization, and antenna design rapidly expanded the scope of this emerging technology. By the 1970s, migratory routes and range sizes of raptors, bats, and small mammals were routinely studied. By the late 1970s, the Argos satellite system allowed global-scale tracking of migratory species (Fancy et al. 1988). These developments established radio telemetry as a central method for studying animal movement, reproduction, and habitat use.

For decades, however, radio telemetry remained largely inaccessible to insect ecology. The challenge lay in the extreme size disparity: although many birds and mammals can easily carry devices under 5% of their body mass, most insects weigh only tens to hundreds of milligrams, rendering early transmitters prohibitively heavy (Kissling et al. 2014). As technology advanced, researchers began pushing telemetry into new frontiers. Wikelski et al. (2006) demonstrated the feasibility of attaching ~0.3 g tags to migratory dragonflies (*Anax junius*), revealing decision rules governing flight direction and stopover use. Pasquet et al. (2008) extended the approach to carpenter bees (*Xylocopa*), quantifying pollen-mediated gene flow over kilometer scales. These pioneering studies demonstrated that, with sufficiently large-bodied taxa, insect telemetry can yield fine-scale ecological insights that would otherwise be impossible to obtain.

Bumble bees soon emerged as another focal group. Hagen et al. (2011) tracked *Bombus terrestris* queens and workers using VHF (very high frequency) radio telemetry and aerial (plane) receivers, documenting landscape-scale movements and resource use. These data revealed the promise of telemetry for studying elusive aspects of *Bombus* ecology, particularly nest location and habitat use. Yet, the method also highlighted persistent constraints: transmitter weight can impair flight, especially in workers; battery life is limited to a few days; and dense vegetation or rugged terrain can quickly attenuate signals (Hagen et al., 2011; Kissling et al., 2014). As a result, most telemetry studies in bees have been limited to small sample sizes, short tracking durations, and an emphasis on queens or large-bodied individuals that can tolerate transmitter loads (Cavigliasso et al. 2020; Kratschmer et al. 2025).

Other technologies have since emerged that complement radio telemetry in bumble bees (reviewed in Mola & Williams 2018). Harmonic radar provides continuous movement tracks within ~1 km of open fields and has been successfully applied to bumblebee foraging studies (Osborne et al. 1999). However, it is limited by its propensity for interference between the receiver and observer. RFID tags, weighing only milligrams, can record repeated nest entries and exits, yielding insights into foundress queen activity, seasonal activity budgets, and high rates of early-season nest failure (Gustilo et al. 2025) if used with already known nests. More recently, automated receiver networks such as the Motus Wildlife Tracking System have demonstrated the potential to scale insect telemetry to regional landscapes, continuously monitoring butterflies and dragonflies tagged with digitally coded nano-transmitters at relatively coarse scales (Knight et al. 2019; Fisher et al. 2021). Together, these complementary methods illustrate a growing toolkit for insect movement ecology, each balancing trade-offs in range, resolution, and weight.

Despite these advances, major gaps persist in our understanding of bumble bee spatial ecology that may be solvable with telemetry. Bumble bees provide critical pollination services in both natural and agricultural systems (Kremen et al. 2002; 2004), yet key aspects of their life cycle, including nesting behavior, overwintering site selection, and early-season queen activity, remain poorly characterized in the wild due to observational constraints (Mola & Williams 2025). Locating nests and overwintering sites, in particular, has long been a limiting step in *Bombus* research (Liczner & Colla 2019), hindering studies of colony success, survival, and habitat requirements. Radio telemetry remains one of the few tools capable of directly locating nests and quantifying individual free-ranging movements.

Here, we evaluate the feasibility of applying radio telemetry to bumble bees (*Bombus* spp.) to address these long-standing challenges. We first tested the physical limits of tag tolerance in multiple Bombus species and castes through controlled mock-tag trials, using morphological traits (body mass, intertegular distance (ITD), and body length) to predict flight success. We then conducted limited field deployments to assess whether VHF telemetry could be used to relocate individuals and ultimately locate nests under natural conditions. We hypothesized that larger-bodied individuals, particularly queens, would be more likely to retain flight capacity after tagging, with ITD as the strongest predictor of tolerance, as it is often used as a proxy for bee size (Cane 1987; Peat et al. 2005). Rather than testing an ecological hypothesis per se, this study serves as a methodological proof of concept, providing foundational insight for future applications of insect telemetry to questions of nesting site selection, overwintering behavior, foraging ecology, and spatial dynamics – all key components of pollinator biology with direct conservation relevance.

2.2 Materials and Methods

This study consisted of two complementary components: (1) mock-tag trials to evaluate morphological predictors of flight following transmitter attachment, and (2) field-based telemetry trials to assess the feasibility of tracking free-flying bumble bees using handheld receivers under natural conditions. All work was conducted during the summer of 2024 in Larimer County, Colorado, using wild-caught bumble bees.

2.2.1 Mock-tag trial design and tag attachment

Mock-tag trials were conducted on the Colorado State University (CSU) campus (Fort Collins, Colorado, USA) from June to August 2024. Wild Bombus individuals were captured opportunistically using aerial nets and plastic vials in flower-rich patches, ensuring representation of all available species and castes. Captured bees were held individually in plastic vials, placed in coolers with ice packs until immobilized (typically 10-30 minutes), and handled under sedation to minimize stress and prevent injury.

Bees were fitted with handmade mock transmitters designed to closely approximate the Lotek NanoPin VHF beeper tags in size, shape, and aerodynamic profile (Figure 1A). Tags were constructed from a 20-gauge steel wire coil core surrounded by an aluminum foil casing with a thin 28-gauge steel wire “antenna” protruding from the posterior end, weighing precisely 140mg. Each mock tag was affixed to the dorsal abdomen using a single drop of cyanoacrylate adhesive (commercial grade “superglue”; Figure 1A), following prior work indicating abdominal placement yields higher flight success than thoracic or ventral placement (Hagen et al. 2011). During placement, bees' wings were gently held away from their body using curved forceps, and mock tags were held in place until the glue was sufficiently dry to avoid wings or legs becoming glued to the bee.

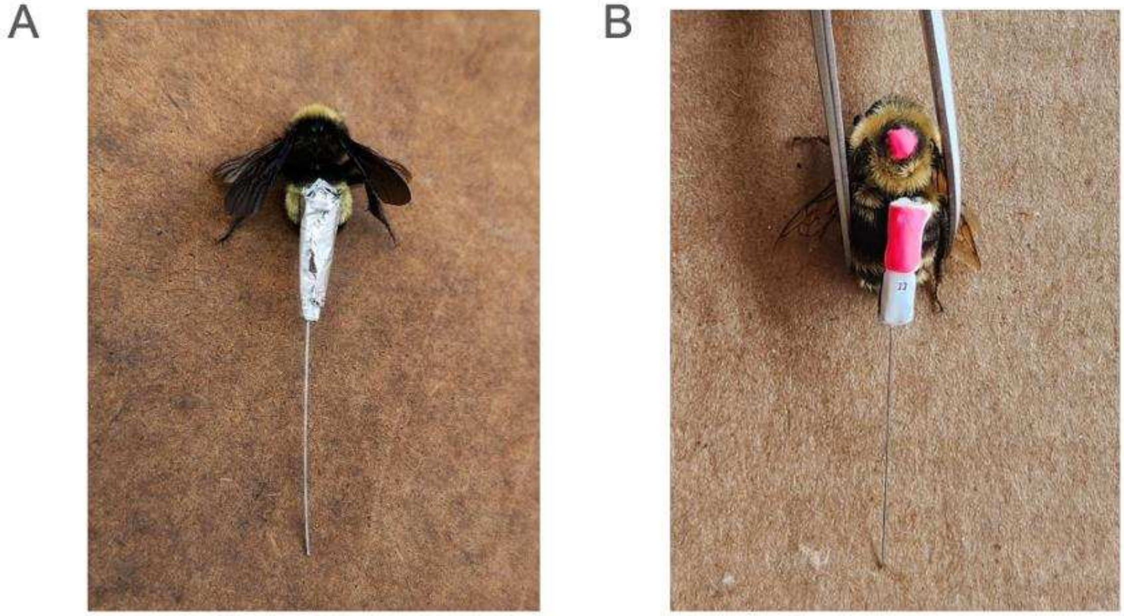

Figure 1. Bumble bees (*Bombus* spp.) fitted with (A) mock radio tags crafted from wire and aluminum, and (B) Lotek NanoPin VHF radio tags.

2.2.1.1 Morphological measurements

We recorded three morphological traits expected to influence tag tolerance: intertegular distance (ITD), body length, and body mass. ITD was measured as the straight-line distance between the tegulae across the dorsal mesoscutum using digital calipers to 0.01 mm. Body length was measured from the anterior clypeal margin to the abdominal apex with the abdomen in relaxed posture, recorded to 0.1 mm. Mass was measured using a portable digital balance (± 1 mg) within 5 minutes of removal from ice. All measurements were taken before paint-marking and tag attachment to avoid artifacts.

2.2.1.2 Flight trials and outcomes

Following tag attachment, bees were positioned upright on a flat surface near their capture location outdoors and observed for up to 10 minutes, or just past 10 minutes if bees began to show signs of flight close to the time cut-off. Behaviors were noted and outcomes were scored as “Fly” (individual successfully lifted off and maintained sustained flight beyond immediate visual range); or “No fly” (individuals unable to achieve or maintain flight within the observation window). Non-flying individuals had their tags gently removed by shaving away at glued abdominal hairs using a razor blade and were re-released; most resumed normal flight within minutes. All bees were marked with a small dot of acrylic paint on the thorax to prevent recapture and retagging.

2.2.1.3 Analysis

We analyzed flight success using generalized linear models (GLMs) with binomial error distribution and a logit link in R version 4.3.2. The binary response variable was flight outcome (fly = 1, no fly = 0). Predictor variables included were body mass (mg), intertegular distance (ITD; mm), and body length (mm). Univariate models were first fit for each predictor individually, followed by a multivariate model including all three predictors. Odds ratios with 95% confidence intervals were calculated for interpretability. Model fit and assumptions were checked using standard diagnostics, and no violations were detected. Information-theoretic model comparison was also used to evaluate whether the multivariate model provided improvement over the weight-only model.

2.2.2 Field telemetry trials

Field tracking was conducted at Ben Delatour Scout Ranch 40.6° N, 105.3° W; elevation ~2000 m) in

Larimer County, Colorado. The site comprises open rangeland interspersed with rolling hills, ponderosa pine stands, shrubby vegetation, and riparian areas adjacent to a small pond and ephemeral creek. Dominant flowering plants during summer 2024 included Cirsium (thistle), Grindelia (gumweed), and Geranium (wild geranium), which supported periodically abundant Bombus foraging activity. The largely open terrain and minimal infrastructure provided favorable line-of-sight conditions for telemetry.

2.2.2.1 Capture, tagging, and release

Bees were netted opportunistically while foraging, chilled in coolers on ice packs until immobilized, and fitted with Lotek NanoPin VHF transmitters (11 x 3 x 3 mm; 140 mg; Lotek Wireless, 2025). Nominal battery life was ~7 days at 12 ms pulse width, with programmable 5-13 second intervals for digitally coded tags. To improve flight ability, transmitter antennas (originally ~15 cm) were shortened to approximately ~10 cm, reducing aerodynamic drag and snag risk, but with the expected cost of reduced detection. Tags were affixed dorsally on the abdomen with cyanoacrylate adhesive (Figure 1B). After tagging, bees were released onto a flat surface near the capture site and observed.

2.2.2.2 Tracking protocol

Telemetry was conducted using SRX-1200 receivers (Lotek Wireless) with a three-element flexible Yagi antenna. Upon release, bearings were immediately taken, and individuals were followed by triangulation using two or three receivers. If signals weakened or were lost, searchers implemented expanding-square or transect sweeps. When still undetected, 200-300 m radial scans were conducted around last known locations, and sites were revisited at 30-60 minute intervals. Each bee was tracked until signals were lost or until the individual could no longer be relocated. All procedures were designed to minimize harm and reduce behavioral disruption. Bees failing to recover from sedation or sustaining injury during handling had tags removed and were euthanized immediately.

2.3 Results

2.3.1 Mock tag trials

A total of 120 bumble bees represented multiple species and castes were mock-tagged during campus trials. Of these, 111 had complete measurements for intertegular distance (ITD), body length, and body mass and were included in the statistical analyses. Flight success was rare overall, with only 12% (13 of 111) of bees achieving sustained flight following tag attachment.

Morphological traits varied substantially across tagged individuals. ITD ranged from 3.4 to 7.3 mm (mean ± SD = 5.0 ± 0.8 mm), body length from 11.2 to 23.1 mm (15 ± 2.5 mm), and body mass from 78 to 476 mg (149 ± 83 mg). Bees that successfully flew were noticeably larger, averaging 5.5 mm ITD, 17.3 mm body length, and 307 mg mass, compared to 4.9 mm ITD, 14.6 mm body length, and 125 mg mass for non-fliers.

Caste composition of the tagged bees was predominantly workers, though several queens and males were also represented. Descriptive plots by caste and species showed that larger individuals, particularly queens, clustered above the ~300 mg threshold associated with flight success, while most workers fell below this limit. These distributions highlight the biological constraints of tag tolerance, with smaller-bodied castes rarely capable of lifting the mock transmitters.

In univariate logistic regressions, each morphological predictor was significantly associated with flight ability. The probability of flight increased with ITD ($-8.9056 + 1.3477 \cdot \text{ITD (mm)}$; $p = 0.003$), body length ($-10.166 + 0.508 \cdot \text{length (mm)}$; $p = 0.001$), and body mass ($-7.223 + 0.0231 \cdot \text{mass (mg)}$; $p < 0.001$).

Threshold estimates indicated that bees heavier than ~310 mg had a ≥50% predicted probability of flight, while very few individuals below 250 mg successfully flew.

When all three predictors were included in a logistic regression, only body mass remained a significant positive predictor of flight ability (Figure 2A). The full-model coefficients were: intercept −8.874; mass 0.0223 (significant); ITD −0.653 (not significant); length 0.320 (not significant). ITD (Figure 2B) and body length (Figure 2C) were therefore not independent predictors once mass was included. The mass-only model was also the best-supported model by AICc, and a likelihood-ratio test showed no improvement from adding ITD and length.

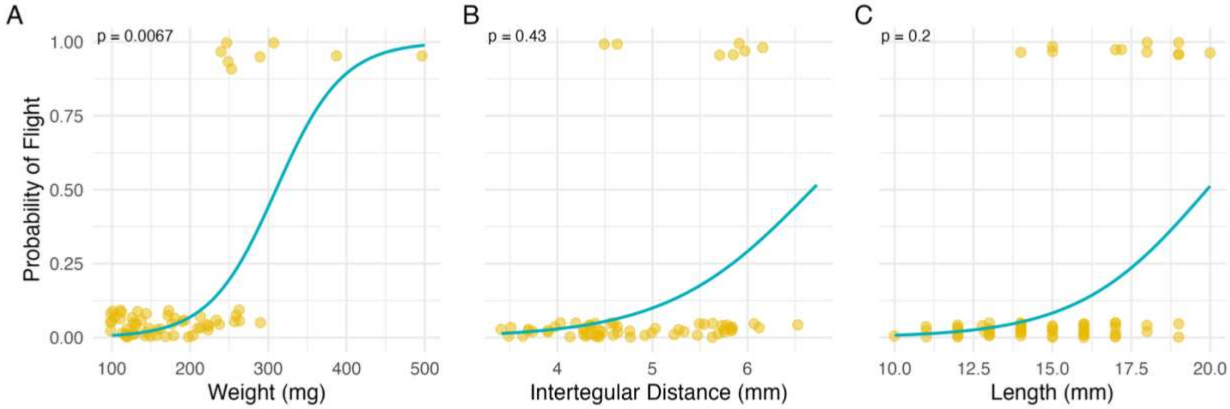

Figure 1. Relationships between morphological traits and probability of flight after tag attachment in mock trials. Logistic regression curves (blue lines) show the relationship between flight success (yellow points) and (A) body weight (mg), (B) intertegular distance (mm), and (C) body length (mm) across individuals tested. Weight was the only significant predictor of flight ability (p = 0.0067), while intertegular distance (p=0.43) and body length (p = .20) were not significant.

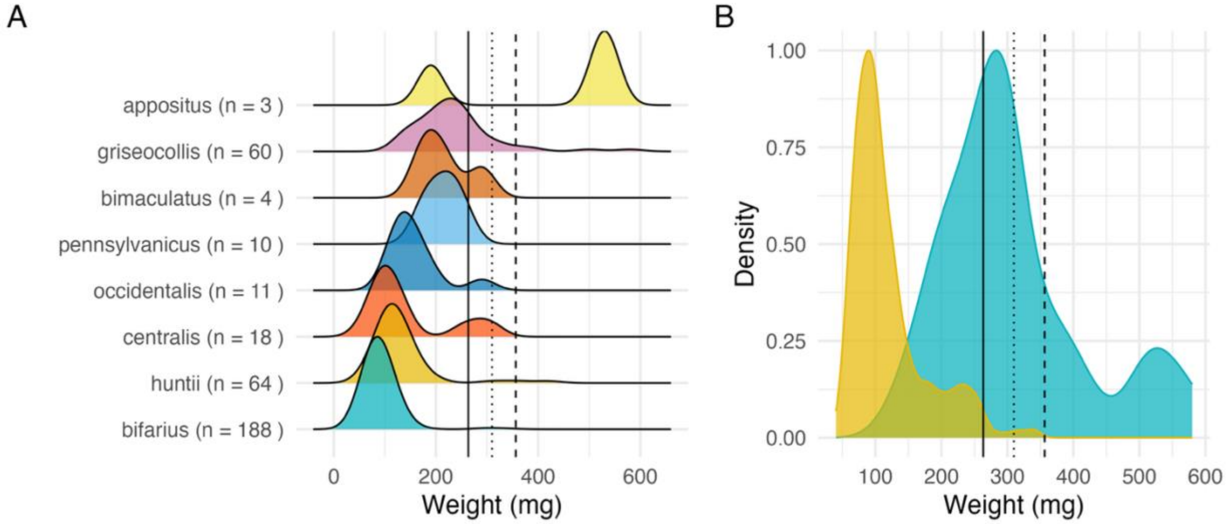

Figure 3. Body mass distributions of all bumble bee species and castes caught and measured throughout the study (n = 358; not all individuals measured were tagged). (A) Ridge density plots of individual weights (mg) for each *Bombus* species, with vertical line markers indicating weight thresholds at which 25%, 50%, 75% of individuals successfully flew with attached tags. (B) Combined density distribution of weights by caste (queens shown in yellow vs. workers shown in blue), showing higher body mass in queens relative to workers. Vertical dashed lines indicate the same weight thresholds as in panel A.

2.3.2 Field telemetry trials

A total of 22 bumble bees were fitted with live VHF transmitters and released under natural conditions at Ben Delatour Scout Ranch. Individuals represented multiple species and castes, but the sample was biased towards larger-bodied bees. Outcomes varied widely following release. Several bees achieved immediate takeoff and sustained flight, while others were unable to become airborne and remained grounded until tags were removed. Overall, fewer than a quarter of tagged individuals flew successfully, and grounded outcomes were most common among smaller workers.

Of those that flew, many bees flew into trees or thatch and remained there for long periods (hours to the following day). Relocation success was low. Signals from most flying individuals were lost within minutes to tens of minutes, typically after rapid directional flights beyond detection range. Only three bees were relocated on the day following their release (~24 hours post-release), representing the maximum tracking duration achieved. None were detected beyond 48 hours.

Signal loss was often abrupt and appeared influenced by topography, vegetation, and antenna orientation. In open terrain, detections extended to several hundred meters, but in shrubby or forested habitats signals weakened quickly and were rarely reacquired. The three multi-day relocations occurred in such habitats, though movements could not be resolved to specific nest sites.

2.4 Discussion

To apply emerging methods such as miniaturized radio telemetry to bumble bee movement ecology, it is important to first establish a methodological checkpoint at which we can evaluate the feasibility of this technology in this study system. Our mock-tag and field telemetry trials converge on a consistent finding: body mass appears to be the dominant determinant of whether a bumble bee can sustain flight when fitted with a VHF radio transmitter. In the mock-tag trials, heavier individuals were far more likely to fly after tag attachment, while smaller workers rarely succeeded. Statistical models confirmed this pattern, with a weight-only model performing as well as or better than models that included intertegular distance and body length. A practical threshold emerged around 310 mg, above which individuals had roughly a fifty percent chance of successful flight, whereas those below 250 mg seldom flew. This simple threshold provides a clear and easily deployable screening criterion for future telemetry studies using the Lotek NanoPin transmitters in bumble bees.

These findings align closely with the broader insect telemetry literature. Early applications of VHF to large insects such as dragonflies (Wikelski et al. 2006) and carpenter bees (Pasquet et al. 2008) demonstrated that tags constituting a substantial proportion of body mass could be tolerated, but only in taxa with powerful flight. The first studies to apply VHF to bumble bees likewise found that only relatively large-bodied individuals, particularly queens and large workers, were capable of carrying transmitters and maintaining flight (Hagen et al. 2011). Our results reaffirm those observations while providing a quantitative threshold for Bombus that can guide practical decision-making in the field. Importantly, they highlight that body mass is a faster and more reliable predictor than intertegular distance or body length, which, although often correlated with size, did not retain independent predictive power once mass was included in models.

The field telemetry trials extend these insights but also underscore the challenges of applying VHF to free-flying bees. Most tagged individuals required long resting periods after tagging or failed to recover and sustain flight while bearing the transmitters. Though some individuals achieved sustained flight immediately after release, relocation success was limited. Signals were typically lost within minutes to tens of minutes, often after rapid, directional flights beyond detection range. Only three bees were relocated the following day, and none were detected beyond 48 hours. Signal loss appeared to be strongly influenced by habitat structure, with shrublands and riparian corridors attenuating signals far more than expected from nominal transmitter range. These outcomes mirror findings from other insect telemetry studies in which dense vegetation, topography, and antenna orientation drastically reduced practical detection distances (Knight et al. 2019; Fisher et al. 2021).

The challenges we encountered are not unique to *Bombus*. Studies tracking invasive Asian hornets (*Vespa velutina*) with VHF transmitters provide a close parallel. Workers carrying tags weighing approximately 280g were tracked back to nests over distances exceeding one kilometer, but success depended on maintaining tag:body-mass ratios below 0.8 and adopting systematic search routes (Kennedy et al. 2018). These results highlight that transmitter weight relative to body size and search strategy together determine outcomes for using telemetry in Hymenoptera. In our case, body mass constrained flight feasibility, as well as terrain and receiving strategy, served as additional bottlenecks for relocation success.

In contrast to these constraints, the use of other tracking technologies may complement VHF telemetry in future studies. Harmonic radar uses a lightweight passive transponder that reflects radar signals at a harmonic frequency, allowing researchers to plot flight paths continuously in real time. This method can track individuals over distances of up to 700–1000 m in open habitats and has been highly effective for studying foraging flights of bees (Osborne et al. 1999; Riley et al. 1996). However, radar units are large, expensive, and immobile; line-of-sight limitations make them unsuitable for cluttered or forested habitats; and only one insect can be followed at a time on the display, although multiple individuals can be tracked sequentially (Mola & Williams 2018). RFID technology offers another complementary tool. Passive microchips glued to the thorax weigh only milligrams and are detected whenever bees pass a fixed antenna, typically at nest entrances or artificial feeders (Streit et al. 2003; Gill et al. 2012; Gustilo et al. 2025). RFID excels at documenting activity budgets, foraging frequency, and seasonal patterns with negligible impact on flight, but it provides no spatial data once bees leave the detection point. Taken together, these complementary approaches - harmonic radar for fine-scale trajectories, RFID for nest activity, and VHF telemetry for relocation across heterogeneous landscapes – provide a growing toolkit for insect movement ecology. Integrating these methods could yield a more complete picture of bee behavior across spatial and temporal scales.

Our study contributes a methodological checkpoint for *Bombus* telemetry, highlighting both what is feasible and where limitations lie. From a practical standpoint, weighing individuals at capture provides a rapid screen, enabling researchers to avoid deploying transmitters on bees that are unlikely to fly. Attachment techniques also matter; minimizing adhesive mass and aligning tags with the body axis can reduce aerodynamic drag, while shortening antennas within manufacturer specifications may further decrease drag and snagging. Environmental conditions at release are equally critical, with warm, calm weather and open release sites providing the best chance of immediate success. Nevertheless, our results suggest that the most significant gains in relocation probability will come not from tag modifications alone, but from receiver strategy. Manual tracking is inherently limited in rough terrain; arrays, vehicle-mounted receivers, or UAV-assisted searches are likely necessary to extend detection windows into the multi-hour or multi-day range achieved in other taxa.

Biological and ecological context also strongly shape feasibility. Queens and large workers are far more likely to exceed mass thresholds than small workers, so species size and seasonal timing determine who can realistically be tagged. Our results indicate a practical even-odds flight threshold around 310 mg, which, given the 140 mg NanoPin, works out to a ~45% tag load. Under a simple normal approximation of our sample (mean 149 ± 83 mg), only ~2.6% of individuals exceed 310 mg, explaining why successful flights were rare. For a typical worker (~149 mg), a tag with comparable (~50%) flight odds would need to be about ~67 mg (0.45 × 149). If we adopt common “safe-load” targets, that implies ~45 mg for a ≤30% load or ~30 mg for a ≤20% load -- i.e., tags roughly 2–5× lighter than our current units. In practice, this means early spring and late-fall queens are the most promising demographic for VHF telemetry with today’s hardware, while midsummer workers are generally too small. These constraints echo broader conclusions that insect telemetry feasibility is highly context-dependent, set by the interplay of body-size distributions, tag design (mass and drag), and environmental conditions.

Our work has limitations. Sample sizes in the field were modest, and we did not experimentally manipulate tag characteristics such as antenna length, adhesive type, or tag-to-body-mass ratio. Future work should address these variables directly, test screening thresholds across species and castes, and incorporate automated receiving infrastructure to assess how much detection duration can be extended. Controlled experiments that vary tag load systematically could also help establish generalized guidelines for feasibility across different pollinator taxa.

2.5 Conclusion

In conclusion, our results underscore two central points. First, body mass is a reliable and quickly measured predictor of tag tolerance in *Bombus* and should be the primary screening metric for future deployments. Second, relocation success in the field depends as much on terrain and receiving strategy as on the bees themselves. VHF telemetry is therefore best viewed as one component of a broader tracking toolkit, to be used in combination with other methods such as harmonic radar and RFID to triangulate bee behavior across spatial scales. By quantifying clear size thresholds for flight, documenting the limits of manual relocation, and situating our work within the broader insect telemetry literature, we provide a detailed baseline for applying VHF telemetry to bumble bees. This study should serve as a practical reference point for future efforts aiming to refine and expand the use of telemetry in pollinator research.

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