

Next-generation colony weight monitoring: a review and prospectus

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Abstract – Healthy honey bee colonies follow predictable patterns of weight change through the season, gaining weight when resources are abundant and losing weight during periods of scarcity. Divergence from this pattern can indicate trouble in the colony, necessitating beekeeper intervention. While colony weight monitoring has long been used to evaluate colony progress and diagnose potential problems, research has been limited by the labor associated with manual weight measurements. The introduction of next generation colony weight monitoring permits the collection of hive weight data continuously and remotely, enhancing the range of questions that can be answered with these data. However, there is currently no central guide for researchers aiming to use hive scales in their research. Here, we review the literature and describe current methods used to process and analyze within-day, or diel, and seasonal colony weight changes. Diel weight dynamics are based around the circadian rhythm of the colony, resulting from the departure and arrival of foragers and the intake, consumption, and dehydration of food stores. Seasonal weight dynamics can be used to assess colony survival and productivity, often in relation to large-scale patterns of climate, landscape, and floral resource phenology. In addition to describing methods, we highlight future applications of hive weight monitoring, including monitoring weight across ecological gradients and physiological time, coupling of weight monitoring with other colony monitoring techniques, and the practical use of weight monitoring in commercial beekeeping operations. This paper serves as a tool for those wishing to conduct research using colony weight monitoring, and guides the future of remote weight monitoring in honey bee research.

hive scale / honey bee / Apis / pollinator / apiculture

1. INTRODUCTION

Happy families are all alike; every unhappy family is unhappy in its own way. ~Leo Tolstoy (1878), Anna Karenina

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While Tolstoy presumably had human families in mind, it is perhaps not incidental that, as a beekeeper, he was well acquainted with another sort of family for which his insight is equally true. The diverse ailments of honey bee colonies lead to vast pathological possibility (Genersch 2010), but healthy colonies are, broadly speaking, all alike. In particular, healthy colonies gain weight during favorable conditions, and heavy colonies survive unfavorable conditions (Döke et al. 2019).

The estimation of weight as an integrative index of colony health and productivity is a standard practice among beekeepers that predates modern weighing technology. In its most basic form, a hive is gently tipped in such a way that an experienced beekeeper can infer whether the colony is relatively strong or weak for a given time of year in comparison to its neighbors. Such qualitative assessment can serve as a quick, though coarse, guide for management decisions in situations that preclude detailed colony inspection.

With the advent of modern weighing devices, however, it became feasible to quantify hive weight and explore more refined questions about colony health and its relationship to internal and external conditions. In one of the first rigorous applications of colony weight monitoring, Hambleton (1925) used hive scales to investigate the role of weather in constraining the ability of honey bees to exploit floral resources. Notably, he remarks that the use of hive scales to track patterns of honey production was already widespread among "the best" beekeepers of his time (Hambleton 1925). Other investigators followed suit, using hive scales to study patterns of honey production and their dependency on conditions within and outside the hive (Mitchener 1947, 1955; McLellan 1977; Szabo and Lefkovitch 1990). These early studies were limited, though, by the mechanical platform scales available at the time, which require a human observer to record each weight reading. This necessity severely constrained the number of colonies and locations that could be monitored simultaneously and imposed a strict tradeoff between colony replication and measurement frequency.

In response to these shortcomings of traditional hive scales, Buchmann and Thoenes (1990) introduced the use of electronic hive scales coupled to data loggers to automate the recording of colony weight data, dramatically increasing both the resolution and the scale at which questions of colony weight dynamics could be explored. This approach was later adopted (Thoenes and Buchmann 1992) and refined (Meikle et al. 2006), establishing the suite of methodologies we term "next-generation" colony weight monitoring.

Since these pioneering studies, nextgeneration colony weight monitoring has been applied in a variety of research contexts with a growing range of methodological adaptations and extensions. Our objective in this review is to synthesize existing methods of nextgeneration colony weight monitoring, providing an organized toolkit for prospective users. We then identify opportunities for refining weight monitoring methods and extending their application to new scientific questions.

2. EXISTING TECHNIQUES AND APPLICATIONS

Colony weight monitoring techniques can be organized into two basic categories: those concerned with diel (within-day) weight dynamics and those concerned with seasonal weight dynamics. Each category is suited to certain kinds of research questions, and each poses distinct challenges.

2.1. Diel weight dynamics

2.1.1. Background

The basis of diel colony weight dynamics is the circadian rhythm of the honey bee colony. Each morning, foragers leave the nest en masse, causing an initial decrease in hive weight that is subsequently reversed as they return to the nest laden with nectar and pollen (Holst and Meikle 2018). Nectar is dehydrated to form honey, first actively by the house bees to which it is transferred and later passively in the comb, causing a gradual loss of weight (Park 1925). Pollen is stored in the colony as bee bread and contributes minimally to weight fluctuation (Anderson et al. 2014). Nectar, honey, pollen, and bee bread are consumed throughout the day, resulting in some weight loss through respiration and defecation. Overall weight change during the day is, thus, an additive result of the departure and arrival of foragers and the intake, consumption, and dehydration of food stores. Daily weight normally peaks at dusk when all surviving foragers return to the nest and add their weight to that of the remaining colony. The processes of dehydration and consumption, however, continue through the night, and hive weight reaches a minimum with the initial departure of foragers the next day.

Studies of diel weight dynamics analyze patterns at the scale of minutes or hours, and they are usually focused on questions of how colony-level behavior is reflected in weight changes. Weight monitoring, much like the waggle dance, provides a window into the "social physiology" of the honey bee colony (Seeley 1995). The basic challenge of diel weight monitoring studies is the detection and interpretation of subtle signals amid the noisy variation of within-day colony weight.

2.1.2. Preprocessing of diel colony weight data

When analyzing diel weight dynamics, seasonal trends in colony weight can obscure the hourly or sub-hourly within-day patterns that are the basis of inference. In general, the first step in diel weight analysis is to detrend each colony weight time series by subtracting a daily running average from each individual weight reading, thus isolating the circadian component of colony weight dynamics (Meikle et al. 2006, 2008). Hourly time series, for example, can be detrended by subtracting from each weight reading a 25-h running average (including the focal reading and the adjacent 12 hourly readings before and after it) (Figure 1).

One difficulty in modeling within-day weight changes is the sensitivity of the data to sources of extraneous variation, whether due to known sources such as precipitation or hive manipulations or due to unknown sources such as possible equipment failures. Recording data frequently, such as every 5 min, makes errors relatively easy to detect. This is because weight changes due to colony behavior in short time frames are usually small. However, frequent data collection results in large data sets which can be more computationally demanding to analyze.

2.1.3. Analyzing diel colony weight data

The circadian periodicity of detrended hive weights allows them to be modeled as cyclical functions of time. Meikle et al. (2008) modeled detrended colony weights using simple sine functions and extracted amplitudes as an index of colony foraging activity. When diel amplitudes are analyzed over seasonal time, they can serve as sensitive indicators of floral resource availability. Since foraging activity responds more quickly than colony weight to changing conditions, diel amplitude dynamics presage cumulative weight dynamics (Meikle et al. 2008, 2016a, b). This provides a useful link between the diel and seasonal scales of colony weight analysis.

Another approach to the analysis of diel weight patterns is to decompose the withinday weight patterns into discrete intervals that can be summarized with linear slope estimates. Meikle et al. (2018) analyzed diel colony weight patterns using segmented regression, a technique that algorithmically optimizes the placement of nodes along a continuous x-axis, then fits linear regressions between nodes such that adjacent regression lines are constrained to connect at their shared nodes (Muggeo 2008). Using this approach, Meikle et al. (2018) estimated the slope of weight change during key intervals corresponding to diel behavioral patterns, including the loss of weight due to departing foragers, the gain of weight due to returning foragers, and the loss of weight overnight due to consumption and evaporation. In

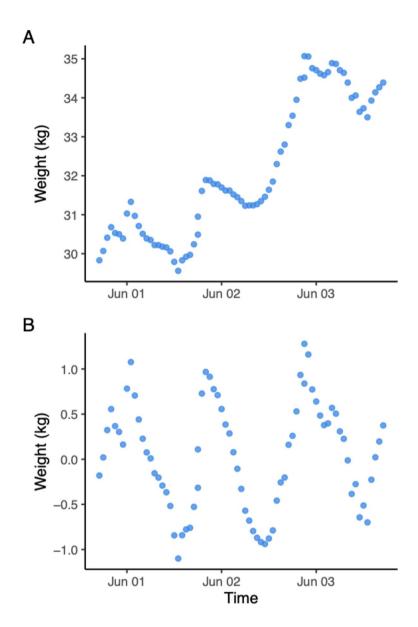


Figure 1. When hourly weight series are detrended by subtracting a running average (A), the circadian rhythm of diel weight dynamics emerges (B). Figure generated from a subset of data collected in 2018 from Philadelphia, PA, USA, with BroodMinder hive scales.

a related study, Holst and Meikle (2018) used segmented regression to characterize a phenomenon they term the "breakfast canyon" — a transient weight loss motif, first described by Hambleton (1925), caused by the initial departure of foragers in the morning. Analysis of diel weight patterns by segmented regression also indicated that both foraging effort (inferred from weight loss due to the initial departure foragers in the morning) and the relationship between foraging effort and cumulative weight gain can differ between colonies deployed for pollination in almond and blueberry production systems (Meikle et al. 2020).

Segmented regression has also been used to estimate the morning forager mass, using three parameters from a regression with four break points: (1) the slope of the segment from midnight until dawn, S_N (hive weight change due to moisture loss at night); (2) dawn break point t_D (start of daily foraging activity); and (3) slope of the 1st segment after dawn, S_M (rate of morning hive weight change) (Meikle et al. 2022). Morning forager mass was corrected for moisture loss thus:

$$\Delta F = S_M (t_{D+1} - t_D) - S_N (t_{D+1} - t_D) \tag{1}$$

with ΔF being the change in hive weight due to forager departure and t_{D+1} being the break point following the dawn break point t_D . A concession was made for unexpected break points: if the first break point occurred before 4AM, the second break point was used as t_D (with no restrictions placed on that second estimate) and the slope of the third, rather than second segment was used as S_M .

Arias-Calluari et al. (2023) combined modeling and statistical approaches to obtain quantitative information about the foraging success of individual bees and the number of active foragers using diel colony weight variations. This model is based on several parameters that include the number of active foragers, the loss of weight due to respiration and bee activities, the mass of food brought by foragers, and the time spent by foragers outside the hive.

One of the key utilities of diel colony weight analysis is detecting discrete events that are masked by long-term weight trends or discarded as noise at the seasonal time scale. Meikle et al. (2016a, b) found that diel weight amplitude is sensitive to both swarm events and pesticide-induced bee kills, each of which results in a signature pattern of dampening in diel weight fluctuations due to the sudden loss of foragers. Similarly, Meikle et al. (2016a, b) and Colin et al. (2019) used diel weight amplitude and breakfast canyon depth, respectively, as indices of sublethal pesticide effects.

2.2. Seasonal weight dynamics

2.2.1. Background

A colony's seasonal weight dynamics are constrained foremost by regional climate. In temperate and subpolar regions, colony development is restricted to a well-defined growing season that begins in late winter or early spring and ends with the onset of cold temperatures in the fall. In the tropics and subtropics, seasonality is defined more by precipitation than by temperature, and drought can function analogously to winter. Within the bounds of climate, seasonal patterns of hive weight are the joint product of colony development and food accumulation, principally honey, with the latter depending jointly on floral resource availability and the foraging strength of the colony (McLellan 1977; Meikle et al. 2008). Positive feedback between these drivers can be expected to cause strong, and lagged, temporal autocorrelation in weight patterns: colonies with abundant food stores can produce more foragers, and colonies with more foragers can accumulate more food, provided that sufficient floral resources are available (Khoury et al. 2013).

Studies of seasonal weight dynamics address variation across days, typically extending over weeks or months, and often involving multiple colonies and sites. The key questions for these studies usually concern colony survival and productivity, often in relation to large-scale patterns of climate, landscape, and floral resource phenology. The basic challenge of seasonal weight monitoring studies is the valid interpretation of complex patterns of colony weight change in response to multiple interacting drivers and in the context of nested study designs (e.g., colonies within sites within treatments).

2.2.2. Preprocessing of seasonal colony weight data

The issue of data quality emerges frequently in seasonal studies of colony weight, largely

because of the inevitable tradeoff between data quality and data quantity. With multiple hives and multiple sites, it quickly becomes impractical to prevent perturbations that can bias weight readings, and studies with high colony replication must often use cheaper and simpler measurement set-ups that are more prone to erroneous readings. In one of the first multi-site, seasonal-scale applications of next generation weight monitoring, Lecocq et al. (2015) relied on collaborating beekeepers to manage 26 colonies distributed across Denmark. An inevitable problem that arises in such a design is the

introduction of management artifacts in colony weight time series due to beekeeping activities (see also Sponsler et al. 2020). Lecocq et al. (2015) mitigated management artifacts by filtering the first-order difference of the bi-hourly time series (i.e., a numerical differentiation, subtracting each reading from the previous one) using a threshold that represented the maximum plausible weight change a colony could experience over a 2-h interval. This approach was later adopted by Sponsler et al. (2020) to address the same problem (Figure 2). This simple filtering technique also corrects the transient reading

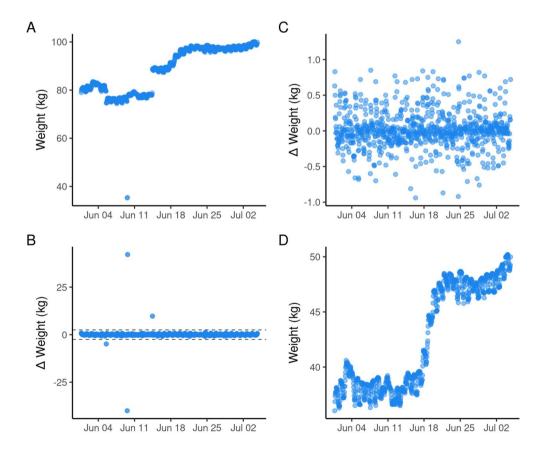


Figure 2. This seasonal colony weight series (**A**) contains level-shift outliers due to a possible swarm event around June 5 and the addition of honey supers around June 15, as well as an additive outlier around June 10 likely due to transient scale malfunction. By taking the first-order difference (**B**) of the raw time series, the original level shift outliers turn into additive outliers, and the original additive outlier turns into a pair of additive outliers. Applying a filter (**B**) to the differences time series, in this case an absolute value of 2.5 kg, both types of outliers can be removed (**C**). Taking the cumulative sum of the clean differenced series produces an outlier-free and zero-based time series (**D**) that can be used for downstream analysis. Figure generated from a subset of data collected in 2018 from Philadelphia, PA, USA, with BroodMinder hive scales.

errors (additive outliers) that sometimes occur in colony weight time series (Sponsler et al. 2020). It does not, however, account for potential time-lagged effects of management on subsequent weight dynamics, an issue that remains unaddressed by existing methods. In some studies, it may also be important to distinguish between management artifacts and swarm events, which could cause similar downward level-shift outliers in a time series; in such cases, close inspection of diel amplitude patterns corresponding to the outlier event may be informative (Section 2.1).

In contrast to the relatively discrete time series generated by daily readings from traditional hive scales, next-generation hive scales produce smooth, continuous time series with hourly or even sub-hourly resolution. In studies of seasonal patterns, researchers may find themselves in the unusual situation of having much more data than they need, which necessitates principled decisions about how to summarize time series in a way that respects the data-generating process while providing clear answers to focal research questions. A common approach when analyzing between-day patterns is to collapse within-day readings into a single daily value, like a 25-h running mean (Lecocq et al. 2015) or a midnight reading (Smart et al. 2017; Sponsler et al. 2020). Such pre-processing enables subsequent analyses to focus on variation at the scale of interest without also having to model cyclical within-day variation.

When extending diel amplitude to the seasonal scale as an indicator of foraging activity (Meikle et al. 2008, 2016a, b), one must choose appropriate time intervals over which to aggregate diel weight patterns. To fit a sine wave, for example, to detrended diel data, a more stable fit can be obtained when multiple days of data are used to fit the model, but this comes at the cost of reduced temporal resolution. In their initial application of this method, Meikle et al. (2008) fit sine waves to 7-day intervals, resulting in weekly amplitude estimates. In a later paper, Meikle et al. (2016a, b) compared the seasonal dynamics inferred from sine waves fit to 7-, 3-, and 1-day intervals and concluded that 3-day intervals provide an acceptable compromise between stability and temporal resolution.

2.2.3. Analyzing seasonal colony weight data

Daily weight readings extending over weeks or months are complex datasets, and difficult decisions must be made regarding how such datasets should be modeled and summarized in the context of a given study. A straightforward approach is to reduce a time series to a single estimate of overall growth, such as by calculating net (Lecocq et al. 2015) or mean (Smart et al. 2017) weight change between the first and last readings of the season. A limitation of this approach is that it ignores the intervening patterns that connect the beginning and endpoint. Cumulative weight change could be the product of steady increase and decrease or alternations of gain and loss, and when such patterns are collapsed into a single summary value, the opportunity to make inference concerning the processes behind those patterns is forfeited. It is not unusual, for example, for a strong colony in a rich foraging landscape to succumb rapidly to an unmanaged Varroa mite (Varroa destructor) infestation late in the year and have its honey stores robbed by neighboring colonies. A single value of net weight loss for such a colony could easily be misinterpreted as an indication of poor resource conditions in the surrounding landscape.

A more nuanced approach is to break a weight series down into time periods of interest and focus on net weight change across these focal intervals (Quinlan et al. 2022). This retains the simplicity of single-value indices of weight change, but it respects the seasonal structure of colony weight dynamics. Focal intervals can be designated a priori (e.g., weight change during May) or they can be determined empirically by identifying meaningful discontinuities in the seasonal time series, either informally by visual inspection of weight curves or by more formal methods such as segmented regression, as discussed previously in the context of diel weight dynamics.

Alternatively, one can embrace the continuous nature of colony weight time series and model them accordingly, albeit at the cost of added model complexity. Generalized additive models (GAMs) are especially promising as a unifying modeling framework for handling colony weight time series (Sponsler et al. 2020), but their application to such

studies is still in its infancy. Unlike conventional regression-based techniques, GAMs model data as a smooth process using flexible splines to capture nonlinear patterns while penalizing spline complexity to avoid overfitting (Hastie and Tibshirani 1990). This aligns well with the goals of seasonal colony weight analysis, where the challenge is typically to extract the smooth processes of floral resource phenology and colony development from amid the noise of daily variation due to effectively stochastic processes like weather fluctuation. GAMs can also accommodate hierarchical data structures (Pedersen et al. 2019), with smooth functions within groups (e.g., hives, sites) modeled as deviations from a global smooth function (Figure 3).

Depending on the hive scale used and its manner of installation in the field, inaccuracies in the absolute value of weight readings can emerge. Some hive scales, for example, are sensitive to a hive's internal weight distribution or to the levelness of the hive stand. These factors can vary across hives and sites and confound inferences based on absolute weight readings. Analyses that focus on the direction of weight change rather than on comparisons of absolute weight across hives are robust to this kind of data quality issue and can yield clear inferences about the timing of nectar flow and dearth periods (Sponsler et al. 2020). Additionally, quality of scales is variable, often directly related to scale cost. Less expensive scales may have batteries that exhaust more quickly or have lower storage capacity compared to more expensive scales. When selecting a scale type for long-term data analysis, these considerations are important.

3. CHALLENGES AND OPPORTUNITIES

Colony weight monitoring is now wellestablished among both researchers and beekeepers, but there remain salient challenges and opportunities to be addressed by future work. We group these under four overarching topics: (1) analyzing weight dynamics across environmental gradients, (2) integrating weight with environmental models, (3) linking weight to other colony monitoring technologies, and (4) applying colony weight monitoring in commercial beekeeping operations.

3.1. Weight dynamics across environmental gradients

Honey bee colony weight dynamics are influenced by biotic and abiotic conditions that differ based on colony location. Researchers may deploy hive scales along a gradient of environmental variables such as agricultural land use, urban-rural gradients, or elevation. Colony weight may then be assessed with patterns of land use change or largescale regional weather and climate trends. Factors including nectar flow and colony productivity could then be compared across a gradient or suite of land use conditions or to describe and predict regional or national variation in such metrics. Remote weight monitoring promotes opportunities for large-scale comparisons of weight change, as demonstrated in a multi-state study in the Northcentral US, integrating the effects of climate, weather, and landscape on colony weight (Quinlan et al. 2022). A similar study aimed to assess landscape influences on food collection and colony weight change, with focus on weather and forest structure (Czekońska et al. 2023). Furthermore, temporal variation of nectar flows along elevational gradients could be detected with colony weight monitoring (Vansell 1928; Bayir and Albayrak 2016). These data could be used to investigate the influence of elevation on the phenological timing of plantpollinator interactions and investigate the effects of climate on these dynamics.

Because climate and weather can have direct effects on colonies through the constraint of foraging activity, as well as indirect effects via floral resource availability, both must be considered when drawing conclusions from colony weight data (Mao and Huang 2009; Sun et al. 2015; Ziska et al. 2016; Lawson and Rands 2019). Weather and climate condition the ability of bees to forage, as bees do not fly when local weather conditions are cold or rainy, and climate drives these trends over years. Previous work has

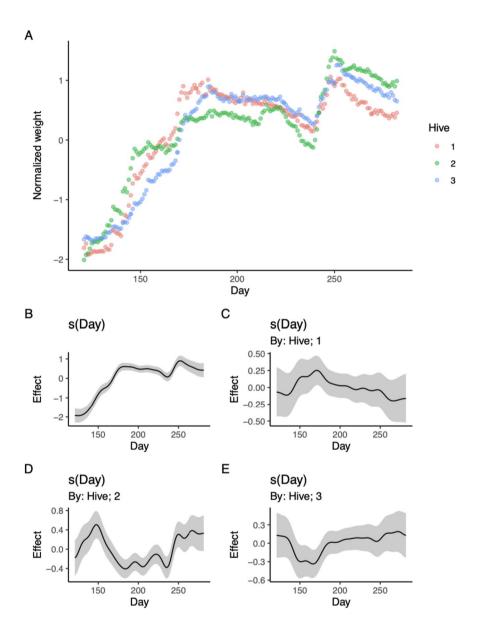


Figure 3. Seasonal weight monitoring studies often involve the replication of hives within sites (**A**), causing non-independence both between measurement-within-hive and hives-within-site. Hierarchical GAMs can simultaneously estimate smooth across hierarchical data structures, such as site (**B**) and colony (**C**–**E**). Figure generated from a subset of data collected in 2018 from Philadelphia, PA, USA, with BroodMinder hive scales.

demonstrated that changing climates modify floral resources by shifting bloom periods (Rafferty et al. 2016) and altering nectar and pollen output

(Scaven and Rafferty 2013). Colony weight monitoring could be used to identify how floral phenology and active periods are shifting over time.

3.2. Integration of weight and environmental models

Hive scale monitoring offers a promising avenue to collect the data required to address the interacting effects of climate, weather, and the environment on colony dynamics. The integration of environmental models with in-hive metrics could be used to make predictions that support pollinators and beekeepers.

Changes in colony weight could be used to model relationships between foraging, colony size, and resource acquisition. In plant systems, a "growing degree day" metric is used to predict plant growth and development under particular weather conditions. Developing the concept of "foraging degree days" as a weather-based measure of suitable foraging periods could be used in beekeeping to better assess floral availability (Szabo and Lefkovitch 1990). These models could help to make more accurate estimates of landscape-level resource availability by comparing foraging degree days with realized floral resources. If a colony has ample opportunity to forage, as determined by foraging degree days, but collects less than expected, it might indicate limited floral availability on the landscape.

The integration of colony weight monitoring with weather and climate models could elucidate the short and long-term effects of these factors on colony weight. The lagged effects of annual weather conditions on colony weight could be better understood by integrating rainfall and temperature models with colony weight. Additionally, weight data could be analyzed with climate models to assess how climate trends are impacting colony weight over multiple years.

Beekeepers could benefit by using results from these models in their management practices. By modeling foraging degree days, beekeepers could more accurately anticipate key events and manage swarms, supplemental feeding, or honey harvesting accordingly. In addition, occasional periods of dearth may be exacerbated by factors such as seasonal or annual drought conditions. In these cases, colonies may require supplemental feeding provided by beekeepers to persist in certain locations and to limit the detrimental effects of robbing behavior among colonies (Downs and Ratnieks 2000).

3.3. Linking weight to other in-hive sensors

Due to the high labor and financial costs associated with the maintenance of honey bee colonies, research often suffers from insufficient colony-level sample sizes. One way to strengthen scientific findings is to verify that the changes expected in a hive are detected across multiple indicator variables (Meikle and Holst 2015). Hive weight, temperature, humidity, CO₂ concentrations, and bee activity can be expected to respond concomitantly to changes in the environment or treatments (Meikle et al. 2022). The intensity and timing of the response are likely to vary, but because many of these variables depend on each other or on similar processes within the hives, strong effects on multiple variables should often be observable.

3.3.1. Temperature

Slow and long-lasting changes in temperature regulation concomitant with changes in weight are expected in unhealthy hives that are unable to grow or maintain a sufficient adult bee population. Small colonies struggle to regulate temperature and accumulate resources (Colin et al. 2021), and very small colonies usually diminish in size until they die, unless a beekeeper intervenes (Dennis and Kemp 2016). In such cases, both temperature regulation and weight gain are expected to further decrease as the population of each new generation of workers shrinks.

Concomitant hive weight and temperature changes may also be expected when the temperature within the hive exceeds what workers consider ideal. In most temperate areas, water is readily available, and bees often collect water promptly (Jones and Oldroyd 2006). Thus, following spikes in temperature, high precision scales may record a rapid increase in weight and relative humidity as bees collect water for evaporative cooling. As the hive returns to the ideal temperature range, any weight increase due to rapid water foraging should cease and weight may decrease due to evaporation. In hot weather,

a lack of rapid weight increase due to water collection could indicate that bees are unable to source water which may lead to death by overheating. If weight increase associated with water collection can be detected using hive scales, they could be the basis for warning systems in hot and arid areas or during heat waves.

3.3.2. CO_2

Analyzing CO₂ concentration together with weight could accelerate research focusing on the regulation of CO₂ within hives. CO₂ production increases with metabolism (Heinrich 1981), so CO₂ concentration may reflect the number of individuals in a colony, changes in bee activity, or basal metabolism (Meikle et al. 2022). During the active foraging season, weight variations are mostly affected by nectar evaporation and foraging activity (Meikle et al. 2018), which makes the detection of food consumption using scales difficult. Rainy days could be used to study CO₂ variations in relation with weight loss as bees generally stay in the hive in these conditions.

In winter, bees consume the honey stores they were accumulated during summer which drives weight change. Food consumption varies according to various factors, including colony size, outdoor temperature, and possibly breeds and subspecies (Norrström et al. 2021). This should ease comparisons of the CO₂ concentration expected from weight loss due to food consumption to actual concentrations of CO₂. This would allow the determination of basic but crucial data on the regulation of CO₂ concentrations, which may play a role in the maintenance of overwintering dormancy (Van Nerum and Buelens 1997).

3.3.3. RFID

RFID (radio-frequency identification) and QR code (quick response code) technologies can track the time at which bees enter and leave the hive (Odemer 2022). Individual bees can be fitted with tags that contain a unique identifier, glued onto their thorax. This, combined with an

antenna for RFID systems or a camera for QR code systems, allows to determine the times at which a bee leaves the hive and comes back. When enough bees are tagged, the changes in departures and arrivals can be compared to hive weight variations. RFID methods, in particular, are now well-established and can be deployed in the field (Colin et al. 2022). The combination of these data with hive weight has the potential to confirm predictions that have been made about bee foraging (Arias-Calluari et al. 2023).

Colonies lose weight in the morning due to a greater number of foragers departing than returning for the first few hours after sunrise (Meikle et al. 2018). Maximum morning weight loss and the rate of weight change have been used to indicate hive activity; however, these variables may be affected by other factors. First, bees commonly remove waste in the morning (Winston 1987), resulting in bees departing the hive that weigh more than their body weight. Second, the average foraging time, trip frequency, and foraging success should influence the rate of weight change and the maximum weight loss since the onset of foraging. Rapid weight loss could indicate not only the presence of diseases increasing waste production but also higher foraging activity. Low maximum weight loss since the onset of foraging could indicate low foraging activity due to a lack of foragers, poor foraging conditions, or the presence of abundant food near the hive.

These questions could be answered by analyzing the common patterns of hive weight changes in combination with data from individual bees equipped with RFID or QR code tags from hives at different locations. Estimates of the number of bees within colonies, of floral resources around the hives, and measures of daily weight change and of the foraging history of a few bees could be combined to better understand which factors contribute most to patterns of daily weight changes. The use of a camera near the entrance may allow, in the future, to further analyze the changes in hive weight in terms of bee behaviors. It may help determine more cryptic causes of weight variations, such as undertaking and water evaporation through fanning, and to differentiate weight gain resulting from pollen or nectar foraging.

3.4. Weight monitoring as a tool for commercial beekeeping operations

Commercial beekeepers manage hundreds or thousands of colonies, often with a high ratio of colonies per beekeeper, making it difficult to closely monitor all hives through the season. Real-time analysis of changes in daily weight variations and overall trends could be used to build health warning tools to support management decisions in commercial operations. Hives experiencing consistent or sudden weight losses and reduced foraging activity at times where they are expected to access ample forage could serve as early indicators of colony failure and give beekeepers more time to intervene to maintain colony strength.

Almond trees located in the central valleys of California bloom in early spring (February–March) and most varieties require cross-pollination to set seed. Beekeepers in the USA relocate millions of colonies to California each spring to satisfy the demand for pollination in almonds. Previous work has shown that continuous weight monitoring can be used to assess colony foraging effort in the fulfillment of pollination contracts in almond orchards (Meikle et al. 2020). In addition to assessing colony performance, colony weight monitoring could be used as a tool prior to contracted pollination to assess colony readiness. Weight monitoring could be added to a regimen to aid in the assessment of colony population size and health before transportation to California and could assist beekeepers in the selection of the best colonies to send to pollination. Migratory beekeeping is associated with stressors such as transportation, nutrition, pests and pathogens, and pesticides (Bruckner et al. 2022; Simone-Finstrom et al. 2016). Hive scales could be used as a tool to monitor the effects of these various sources of colony stress. Continuous colony monitoring before, during, and after pollination service would allow comparison with colonies not moved for pollination to identify key differences in colony growth and performance associated with migratory beekeeping and pollination. Additionally, weight data can be used to provide information on Varroa destructor population dynamics. Onset of brood rearing, detectable with hive scales, is closely tied to season-long *Varroa* infestation levels, permitting beekeepers to take early action toward mite control.

Indoor overwintering of commercial honey bee colonies in temperate climates has been conducted for more than 100 years (Doolittle 1902; McCutcheon 1984) to improve overwintering survival and, more recently, in preparation to meet early spring pollination contracts for almonds in California. Overwintering colonies in temperaturecontrolled facilities offers an attractive means for providing the larger colony population sizes sought after by almond growers (DeGrandi-Hoffman et al. 2019) as well as for beekeepers living in northern latitudes with very cold winters (Hopkins et al. 2021). The addition of weight monitoring to indoor overwintering operations presents an opportunity to deliver more successful colonies to spring pollination contracts. Continuous weight monitoring could serve as an early indicator of trouble in colonies, alerting beekeepers of insufficient food stores or low colony population sizes.

4. CONCLUSION

Colony weight monitoring exploits the predictable patterns of daily and seasonal honey bee colony dynamics to better understand colony health and behavior. Through the introduction of next-generation weight monitoring, researchers can ask questions at spatial and temporal scales that were previously impossible. Here, we review the existing literature on next-generation weight monitoring, exploring the differences in methods for diel and running weight analyses. By outlining the procedures and methods that have been developed for each type of data, we provide a tool for those wishing to use hive scales in research. We look forward at where we believe there is research opportunity, highlighting questions that can be asked and biological phenomena that can be assessed with colony weight monitoring, as well as opportunities for developing methods to better support the needs of commercial beekeepers.

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AUTHOR CONTRIBUTION

HMS, TC, HGD, GQ, AS, WM, DS contributed ideas; HMS, TC, HGD, GQ, AS, WM, DS wrote the manuscript; HMS, TC, HGD, GQ, AS, WM, RJ, DS revised the manuscript. All authors read and approved the final manuscript.

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DATA AVAILABILITY

Data used to generate figures in the manuscript is available in the GitHub repository (https://github.com/spons lerdb/nextgen_wt).

CODE AVAILABILITY

Code used to generate figures in the manuscript is available in the GitHub repository (https://github.com/ sponslerdb/nextgen_wt).

DECLARATIONS

Ethics Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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