

## ARTICLE

## Methods, Tools, and Technologies

## Evaluating the foraging performance of individual honey bees in different environments with automated field RFID systems

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## Abstract

Measuring individual foraging performance of pollinators is crucial to guide environmental policies that aim at enhancing pollinator health and pollination services. Automated systems have been developed to track the activity of individual honey bees, but their deployment is extremely challenging. This has limited the assessment of individual foraging performance in full-strength bee colonies in the field. Most studies available to date have been constrained to use downsized bee colonies located in urban and suburban areas. Environmental policy-making, on the other hand, needs a more comprehensive assessment of honey bee performance in a broader range of environments, including in remote agricultural and wild areas. Here, we detail a new autonomous field method to record high-quality data on the flight ontogeny and foraging performance of honey bees, using radio frequency identification (RFID). We separate bee traffic into returning and exiting tunnels to improve data quality solving many previous limitations of RFID systems caused by traffic jams and the parasitic coupling of RFID antennae. With this method, we assembled a large RFID dataset made of control bee colonies from experiments conducted in different locations and seasons. We hope our results will be a starting point to understand how ontogenetic and environmental factors affect the individual performance of honey bees and that our method will enable large-scale replication of individual pollinator performance studies.

## KEYWORDS

*Apis mellifera*, bee longevity, flight ontogeny, foraging performance, pollination performance, radio frequency identification (RFID), temporal polyethism

## INTRODUCTION

In much of the industrialized world, the health of pollinating insects is declining at a rate unsustainable for both the crop pollination industry and the environment

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(Biesmeijer et al., 2006; Potts et al., 2010). Honey bees have received the most attention, because colony losses have dramatically increased in recent years and they are the main pollinators of many food crops. The weakening of honey bee colonies is attributed to numerous stressors, including commercial pollination practices, pesticides, pests, pathogens, and environmental change (Alger et al., 2018; Goulson et al., 2015; Henry et al., 2012; Le Conte et al., 2010; Prado et al., 2019), with the parasitic mite *Varroa destructor* likely playing an important role through virus transmission (Le Conte et al., 2010; Rosenkranz et al., 2010). Colony failure is not a trivial problem, and urgent research is being undertaken to model the impacts of these various stressors on colony function (Becher et al., 2014; DeGrandi-Hoffman et al., 1989; Perry et al., 2015; Russell et al., 2013; Schmickl & Crailsheim, 2007; Torres et al., 2015). The response of bee colonies to stress has been found to be nonlinear due to the complex feedback systems, which exist within a bee society (Barron, 2015). However, current understanding and environmental policy-making is limited by a lack of large high-quality datasets on the performance of honey bees in the field.

Colony performance is highly dependent on the capabilities of the foraging force, with foraging representing a key behavioral state for any individual bee (Barron et al., 2002). Worker honey bees adopt different tasks as they age to facilitate the division and optimization of labor. Classical ethological studies have termed this age-based division of labor as “temporal polyethism”. A worker bee typically begins by performing in-hive tasks and ends with foraging (Seeley & Kolmes, 1991). Delaying foraging increases the worker’s life expectancy, as it is the riskiest and most energetically demanding task (Woyciechowski & Morón, 2009). The timing of the behavioral transition to foraging is extremely plastic, allowing the hive to regulate the foraging force and overall collection of nutritional resources (Capaldi et al., 2000; Capaldi & Dyer, 1999; Huang & Robinson, 1996, 1999). From a mechanistic perspective, the transition to foraging is regulated socially by pheromones, with a large successful foraging force inhibiting younger bees from becoming foragers (Leoncini et al., 2004). It is also thought to be regulated seasonally such that foraging onset is inhibited prior to winter (Huang & Robinson, 1995) and physiologically so that poor nutrition or health accelerates the onset of foraging (Fahrbach & Robinson, 1996; Goblirsch et al., 2013; Schulz et al., 2002).

The first flights undertaken by a bee are infrequent and short, being known as “orientation” flights. These flights allow bees to learn their surrounding landscape, before transitioning to a foraging role (Capaldi et al., 2000; Capaldi & Dyer, 1999; Colin, Meikle,

et al., 2019; Requier et al., 2020). Prior studies have argued that the age at onset of foraging is a critical parameter influencing colony and forager performance (Colin, Meikle, et al., 2019; Henry et al., 2015; Perry et al., 2015; Prado et al., 2020; Requier et al., 2020). Stressors accelerate the onset of foraging, which can damage colony health and performance by reducing the population of bees engaged in-hive tasks such as brood rearing (Beshers & Fewell, 2001; Leoncini et al., 2004; Schulz et al., 2002; Toth et al., 2005). Some studies have suggested that bees that begin to forage precociously perform poorly as foragers (Colin, Meikle, et al., 2019; Prado et al., 2020). According to predictions from mathematical models, this could establish a destructive positive feedback loop, which compounds the effects of stress on foragers and the overall demographic balance of the colony (Perry et al., 2015). However, very little data are available to date to check these predictions.

Efforts to model honey bee colony function and temporal polyethism have been restricted by a lack of field data required to estimate the essential parameters for many models (Becher et al., 2014; Colin et al., 2018; Khoury et al., 2011). Although the development of counters to measure bee traffic date back to 1925 (Odemer, 2022), until recently, critical measures such as bee longevity, flight ontogeny, and flight behavior could only be estimated by error-prone and arduous manual observations (Winston, 1987). The use of radio frequency identification (RFID) tags and Quick Response code (QR code) has revolutionized data collection for bee research (Odemer, 2022). The use of such systems is, however, limited by a lack of a readily available system on the market, poor tag detection accuracy, and difficulty analyzing large and noisy datasets (Colin, Meikle, et al., 2019; Requier et al., 2020).

RFID was the first technology developed to automatically identify individual bees (Decourtye et al., 2011). Small passive tags can be attached to the thorax of bees, giving each individual a unique identifier. The tags are read by one or several antennae placed at the entrance of the hive, to record when the bee leaves or returns (Decourtye et al., 2011).

RFID technology has been applied to a wide range of bee studies, with a strong focus on investigating the impact of stressors on bees. RFID-based studies have investigated the effects of pesticides such as neonicotinoids (Colin et al., 2021; Colin, Meikle, et al., 2019; Decourtye et al., 2011; Henry et al., 2012; Hesselbach et al., 2020; Monchanin et al., 2019; Schneider et al., 2012), pathogens such as deformed wing virus and nosema (de Guzman et al., 2017; Dosselli et al., 2016; Lach et al., 2015), modified agricultural environments, climatic conditions (Evans et al., 2019; Gregorc et al., 2012; He et al., 2016), and nutritional preferences and foraging behavior (Bordier

et al., 2018; Chang et al., 2015; He et al., 2013; Perry et al., 2015; Søvik et al., 2015).

There are still some significant limitations to the use of RFID. Most studies to date have been conducted under laboratory conditions utilizing small hives, which are only 3%–15% the size of a commercial hive (Bordier et al., 2018; Chang et al., 2015; Evans et al., 2019; Hesselbach et al., 2020; Lach et al., 2015; Perry et al., 2015; Tenczar et al., 2014). Although these hives are easier to use with RFID, they provide a limited representation of how a full-strength hive (>10,000 bees) may deal with stress.

Small RFID tags with limited range must be utilized to avoid disrupting bee movement and behavior. Tags must pass within millimeters of an antenna to be detected. To maximize detection, the hive entrance must be modified to incorporate RFID antennae. This has commonly been achieved with tunnel or tube entrances, which only allow a small number of bees to pass the antenna at one time (Bordier et al., 2018; Dosselli et al., 2016; He et al., 2013, 2016; Hesselbach et al., 2020; Tenczar et al., 2014). Although effective for small laboratory hives, this is not suitable for full-strength hives with high bee traffic and can prevent hive fanning and hygiene behaviors (Requier et al., 2020). As an alternative, larger double-antenna entrances can be utilized, but these entrances need to be long to prevent parasitic antennae coupling in which the antennae activate each other yielding useless data (Hirsch, 2019). Within longer entrances, bees can reverse path before being detected which complicates data analysis.

While not always reported, the detection accuracy and tag retention of RFID systems have typically been poor, with often only 24%–46% of tagged bees making discernible foraging trips (Bordier et al., 2018; de Guzman et al., 2017; Dosselli et al., 2016; Evans et al., 2019; Lach et al., 2015). This can be attributed to tags detaching, premature deaths, and missed detections. A formal comparison of RFID tag performance has not been conducted to date, with the understanding of system accuracy limited by the lack of methods for filtering and analyzing large RFID datasets.

In this study, we address previous limitations and present an autonomous solar-powered RFID system capable of remote field deployment on full-strength bee hives. We compare the performance of RFID tags and detail a “maze” hive entrance to separate outgoing and incoming bees. We provide a comprehensive R code to enable the filtering and analysis of RFID data. We present a large RFID dataset gathered using these tools (from Colin et al., 2021; Colin, Meikle, et al., 2019; and two unpublished datasets). We then quantify the foraging performance of bees and examine whether there is an

optimal age of foraging onset. We provide measures of the ontogeny and foraging performances of individual bees to aid the development of mathematical models of honey bee colonies. We discuss how these data and new RFID methods can improve our understanding of honey bee colony function.

## METHODS

### Datasets

The data and the code are available in Dryad (<https://doi.org/10.5061/dryad.83bk3j9s6>). Here, we utilized data collected from the control colonies of four different experiments:

#### Sydney summer

These data were collected from two control hives, which were used in a study examining the impact of imidacloprid on bees (Colin, Meikle, et al., 2019). The hives were established in November 2017 at Macquarie University (Sydney, Australia, latitude: 33.7679, longitude: 151.1132) and housed in Langstroth wooden boxes. These two colonies were healthy with no abnormal levels of diseases or pests, and one APITHOR trap was added to each hive to prevent hive beetle outbreaks, common in Sydney. No previous treatments were performed on the colonies, but bees were fed sucrose syrup for 6 weeks, after which frames of capped brood with emerging bees were brushed free of adult bees and held in an incubator (34°C) overnight. The next day, newly emerged bees were tagged with Invengo XCTF-8018 tags using glue (Uhu Superglue Ultra-Fast) and placed in a “common-garden” RFID hive established at Macquarie University in January 2018 (Table 1).

#### Sydney winter

These data were obtained from six healthy control hives with no abnormal levels of pests or diseases, which were used in a study examining the impact of miticides on bees (Colin et al., 2021). They were established in November 2017 at Macquarie University (Sydney, Australia, latitude: 33.7679, longitude: 151.1132), with one Apithor trap per hive to prevent hive beetle outbreaks, common in Sydney. Bees were sampled and tagged as for the Sydney summer dataset and added to a common garden indoor hive (Table 1).

**TABLE 1** Number of control hives and bees in each dataset

Location	Experiment	Hive label	No. tagged bees	Tagging begins	No. successfully detected bees
Hobart	Summer	5A	150	10 December 2019	130
Hobart	Summer	6B	150	10 December 2019	111
Hobart	Spring	2A	110	24 September 2019	91
Hobart	Spring	5B	110	24 September 2019	95
Sydney	Summer	1A	300	13 April 2018	274
Sydney	Summer	2B	301	13 April 2018	290
Sydney	Winter	2	100	2 May 2018	95
Sydney	Winter	5	50	2 May 2018	49
Sydney	Winter	b	50	2 May 2018	48
Sydney	Winter	c	50	2 May 2018	49
Sydney	Winter	l	5	2 May 2018	4
Sydney	Winter	o	32	2 May 2018	31

## Hobart spring

These data were collected from two control hives used in a study examining the impact of protected cropping on honey bee foraging within sweet cherry orchards. In September 2019, two healthy hives with no previous treatment and no abnormal levels of pests or diseases were equipped with an RFID system at the University of Tasmania (Sandy Bay, Australia, latitude: 42.9998, longitude: 147.1014). On 24 September 2019, a frame with emerging adults and more than 100 capped brood was brushed free of bees and placed in a dark incubator for 20 h at 34°C. Newly emerged bees were tagged with RFID tags attached with Cyberbond 2610 superglue (EAL, Australia). Tagged bees were returned to their original hives. On 8 October 2019, both hives and all RFID equipment were transported to Hansen Orchards (Tasmania, Australia) and placed in an open field neighboring a netted cherry orchard. Movement of the hives corresponded with the flowering window of the cherry orchard. The hives were moved back to the University of Tasmania's apiary on 3 November 2019. Data were collected until 5 December 2019.

## Hobart summer

The Hobart summer dataset contains data from two control hives used in a study investigating the impact of carrot pollination on bee health and foraging. Two healthy commercial RFID-equipped bee colonies with no previous treatment or abnormal levels of pests or diseases were maintained at Richmond (Tasmania, Australia,

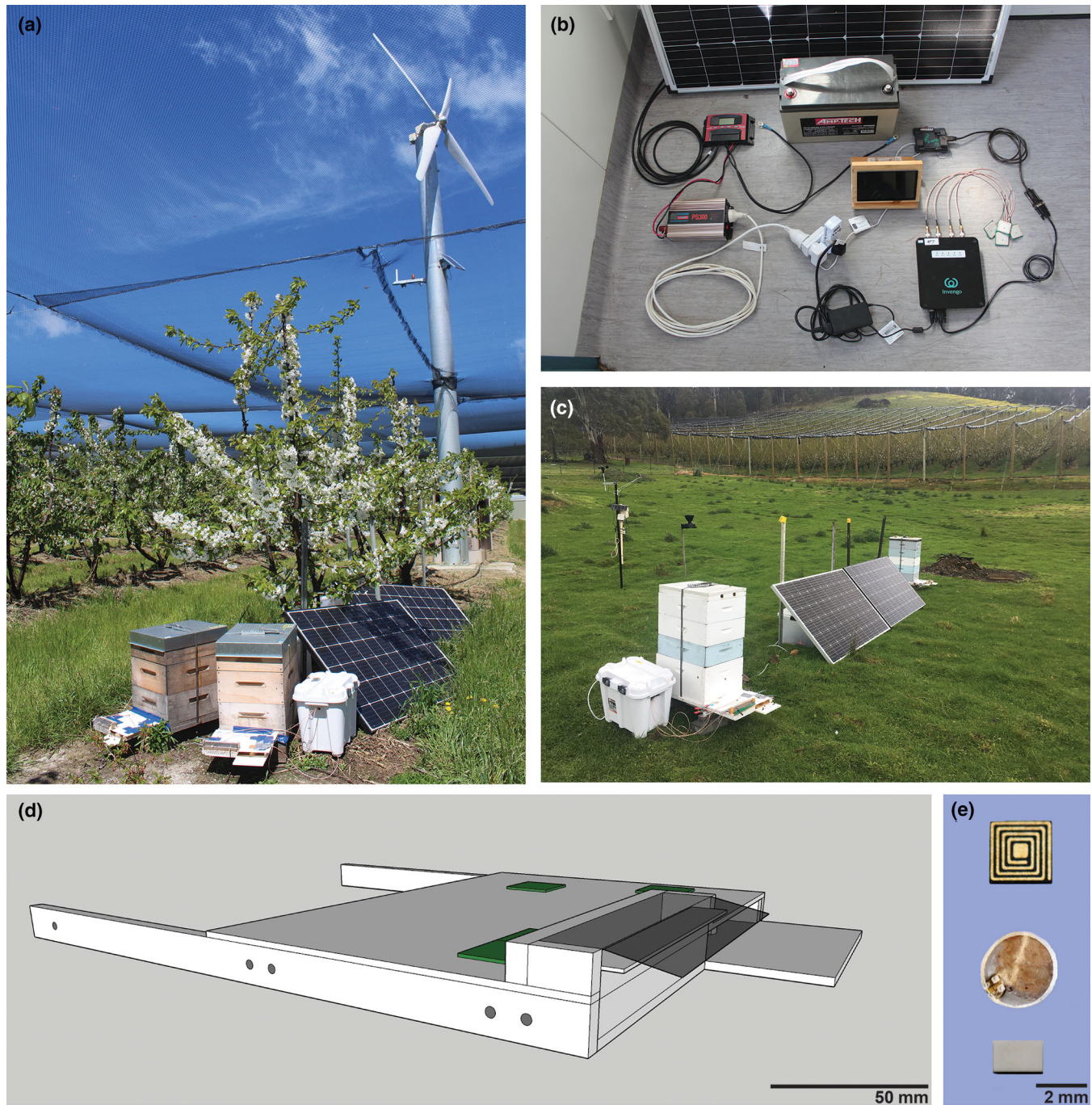
latitude: 42.7101, longitude: 147.5188). Two frames of emerging brood were removed from each hive on 9 December 2019 and incubated overnight at 34°C. Emerging bees were tagged as described in the spring dataset and added back to their respective hives (Table 1). On 27 December 2019, the hives were transported to a mixed cropping property in Orierton (Tasmania, Australia). The hives were positioned close to a carrot crop, after which they were moved back to Richmond on 3 February 2020, where they continued to be monitored until the 3rd of March 2020.

## RFID system

The RFID system used for the Sydney summer and winter datasets is fully described in Colin, Meikle, et al. (2019). The RFID system for the Hobart spring and summer datasets involved improvements detailed in Appendix S1 and Dryad for field deployment. Briefly, this system used an Invengo XC-RF807 reader (Invengo, China) connected to four ABRACON ARK4065-S915A UHF RFID ceramic patch antennae.

Hives were fitted with modified “maze” entrances, which separated exiting and returning bees into different pathways equipped with RFID antennae (Figure 1d). A series of 15-min visual counts were conducted over 4 days to determine the effectiveness of the maze for controlling bee movement. Nearly all bees were observed to move in the correct direction with 99.91% (2250/2252 events) leaving the hive via the exit pathway and 99.71% (4411/4424 events) returning via the entry. The system's detection accuracy was verified by tagging 25 bees and observing





**FIGURE 1** (a) Autonomous, solar-powered RFID system, seen here in an orchard with a weather-proof box containing the electronics, and modified RFID entrances. (b) The power and RFID systems (annotated picture in <https://doi.org/10.5061/dryad.83bk3j9s6>). (c) Field RFID system deployed at another site. (d) Modified hive entrance used to separate bee traffic. Departing bees are funneled to the left by the transverse bar, which separates them from returning bees. Bees must walk under an antenna before exiting through a flap door made of flyscreen mesh. The exit flap is pushed open when exiting but does not allow bees to return. Returning bees land on the longer entrance board on the right and must walk under one of two RFID antennas to enter the hive. Small platforms directly beneath each antenna slow the bees and bring tags within 5 mm of the antenna. Full detail including videos and 3D model with dimension are given in <https://doi.org/10.5061/dryad.83bk3j9s6>. (e) Three types of RFID tags were tested: Hitachi IM5-PK2525-R (top), Invego XCTF-8018 (middle), and Murata LXMS21NCNH-147 (bottom). Murata tags had the best detection rate (see Appendix S1 and <https://doi.org/10.5061/dryad.83bk3j9s6>).

them visually for approximately 1 h per day for 6 days, while also recording RFID detections. Comparing our visual observations with the RFID data showed that

90.5% (57 of 63 observed events of a tagged bee walking under the antenna) of the tags were detected by the antennae as a bee walked under.

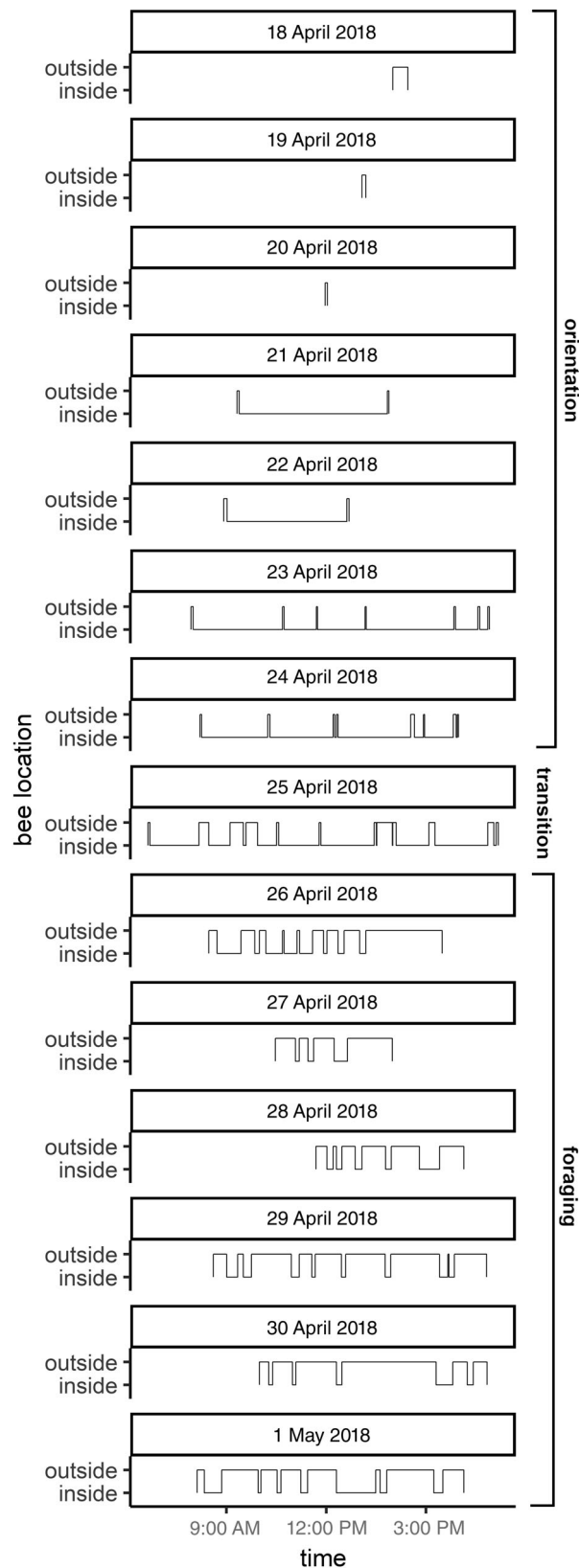
In the Sydney datasets, systems were powered by mains electricity. In the Hobart spring and summer datasets, each RFID system had an autonomous power supply from a 300 W solar panel (TALESUN TP660M-300) wired to a Powertech 12-V 30-W MPPT Solar charge controller (Figure 1a–c). The charge controller was connected to a 120 AH 12-V AGM Deep cycle battery (Marshal AT121000DS) and an Excelsior PS300/12 12-V 600-W pure sine wave inverter. The battery and charge controller were housed in a 120 L tub, with access holes for wiring. The reliability of the system was field tested, with the longest test exceeding 2 months of continuous operation. The system was capable of running uninterrupted on 5 h of sunlight per day, including in shaded orchards. The maximum power consumption of the RFID reader was approximately 22 W while detecting tags. The batteries used in our system provide approximately 2 days of backup power, with scalability for extra panels or additional/larger batteries as required.

## RFID tags

The Sydney datasets used Invengo XCTF-8018 tags, which can easily be damaged, potentially decreasing estimates of bee performance and longevity. A small experiment to compare three RFID tags was realized at the University of Tasmania. Bees were equipped with Hitachi IM5-PK2525-R, Invego XCTF-8018, or Murata LXMS21NCNH-147 tags (Figure 1e). Murata tags remained in the system significantly longer than the two other brands (Appendix 1 and Dryad repository). These tags are smaller and less likely to affect bee movement. We used Murata LXMS21NCNH-147 tags in Hobart (dimensions:  $2.0 \times 1.25 \times 0.55$  mm, read range: 10 mm, UHF band: 865–928 MHz, Protocol: ISO/IEC 18000-63, Electronic Produce Code: global Gen2 V1.2.0, EPC: 256 bit Read & Write) and recommend this tag or similar ones for future work. The market for small RFID chips continues to grow, and although specific tags may disappear from the market, they are likely to be replaced by similar tags in the future (e.g., LXMSJZNCMD-217, dimensions:  $1.2 \times 1.2 \times 0.55$  mm, read range: 10 mm, UHF band: 865–928 MHz, Protocol: ISO 18000-63/Electronic Produce Code global Gen2V2 Compliant, EPC: 128-bit Read & Write).

## Data processing

The RFID and QR code datasets require extensive filtering before a bee's flight history can be reconstituted (Figure 2).



**FIGURE 2** Example of an individual bee's flight record, after filtering. Note the transition between a few short orientation flights in the afternoon to a larger number of longer foraging flights starting in the morning from 25 April.



We provide a detailed method to filter and analyze large RFID datasets in R (see <https://doi.org/10.5061/dryad.83bk3j9s6>). Briefly, in this procedure, we first joined the RFID data to metadata manually associated with each individual tag (date of tagging, treatment, and hive of origin). We then selected one detection of the same tag per minute. Rapid consecutive detections of the same tags are often a result of bees lingering under the antennae. Tags that were only detected once were excluded, because these bees were likely unable to fly or lost their tag. Consecutive entrance recordings or consecutive exits were removed, so that only exit–entrance sequences remained, which could be converted to foraging trips.

Trips of unrealistic duration were then removed. We filtered out trips shorter than 2 min (based on measures from Capaldi et al., 2000 corrected for our longer entrances) and longer than 10 h. Trips of less than 2 min are likely due to bees walking back inside without flying. Our observations showed that trips longer than 10 h occur when bees stay outside overnight, which can happen in cold weather when bees fail to return before the temperature decreases in the evening. We did not consider these flights a matter of interest for the present study, but these filters could easily be changed (see <https://doi.org/10.5061/dryad.83bk3j9s6>).

The daily time of first trip, number of trips, average duration, and total cumulative duration of trips performed by each bee were then calculated. These variables can be used to determine when individual bees transition from performing orientation flights to undertaking foraging trips (Colin, Meikle, et al., 2019). Colin, Meikle, et al. (2019) utilized a linear discriminant analysis to show that simple thresholds based on these criteria allow identification of when individual bees start foraging.

In this study, there was considerable variation in the timing of orientation flights between experiments, which we attributed to flights occurring later in the day during colder seasons. To address this, we used the total time spent outside of the hive on a single day by individual bees as the measure for a transition to foraging. We considered that bees became foragers when they spent more than 20 min outside the hive in a single day. This threshold was determined using a test dataset from Colin, Meikle, et al. (2019), which contains manually detected dates of transitions to foraging for 29 bees. We found this single criterion was sufficient to date the transition to foraging with a 79% accuracy with 0-day error, 92% accuracy with a  $\pm 1$ -day error, and 100% accuracy with a  $\pm 4$ -day error. Note that an alternative method has recently been made available as an R package (Requier et al., 2020; Requier & Rebaudo, 2020). Finally, bees that have never performed foraging trips were only kept in the survival

analyses and removed from other figures and analyses as they may correspond to lost tags and not bee deaths. These can be easily added back into the figures and analyses (see <https://doi.org/10.5061/dryad.83bk3j9s6>).

## Effect of age at foraging on number of foraging trips and survival

We considered three different methods of estimating an optimal age at onset of foraging for bees: (1) 14 days old, derived from Perry et al. (2015), (2) the average age at onset of foraging for each hive, and (3) the average age at onset of foraging for the top 25% bees, which performed the most trips in their lifetime. Such bees have been termed “elites” (Tenczar et al., 2014). We calculated the deviation between the age at onset of foraging of each bee and the three optimal age estimates (Table 2).

We then built linear mixed models for each optimal foraging age estimate. The logarithm of the lifetime number of foraging trips was the response variable, and the interaction between the deviation from the optimal age at foraging (in days) and the sign of the deviation was explanatory variable with hive as a random effect. A null deviation from optimal age at foraging, representing bees who started foraging at the optimal age, was always considered positive. This arbitrary choice had no influence on the results (see <https://doi.org/10.5061/dryad.83bk3j9s6>).

Models were fitted using lme4 v1.1-23, *p* values obtained with lmerTest v3.1-2, residual plots built with DHARMa v0.3.1, and figures using ggplot2 v3.3.1. We observed deviations from the assumptions but considered these were small enough to not affect the robustness of our analyses. Alternative analyses (mixed regression with deviation from optimal age as a polynomial of second order, and mixed regression with deviation from optimal age as an absolute value) are available in the

**TABLE 2** Estimates of age at foraging with the two methods for each dataset. Perry et al. (2015) used 14 days in their model (see Figure 6).

Dataset and hive ID	Hive average (days)	Elite average (days)
Hobart summer 5A	19.76	15.11
Hobart summer 6B	15.06	14.42
Hobart spring 2A	22.09	30.5
Hobart spring 5B	23.31	23.33
Sydney summer 1A	9.83	10
Sydney summer 1B	10.19	11.22
Sydney winter, hives pooled	21.85	17.25

supplementary code and data (<https://doi.org/10.5061/dryad.83bk3j9s6>) and gave similar results.

To test the effect of the age at onset of foraging on the survival rate, we calculated the time to last detection after onset of foraging in days and the total foraging flight time after onset of foraging. Bees from all datasets were pooled together and grouped by age classes of 4 days to ensure sufficient sample sizes for survival analyses and simplify representation. Kaplan–Meier survival curves were built using survival v3.1-12 and survminer v0.4.7. Pairwise comparisons were computed using the survminer package.

## RESULTS

From the 12 colonies utilized, 582 bees performed at least one flight. Data from Sydney winter were pooled due to the small sample size in hives. Thus, we present data of bees from six individual hives and one pool of six hives.

### Estimation of parameters relevant to bee models

We measured the age at onset of foraging, number of flights, average duration of flights, total cumulative flight time, and lifespan of individual bees from these hives (Tables 3 and 4). These can be used to enrich current bee models that are often lacking empirical data.

### Age at onset of foraging

The average age at onset of foraging varied from 9.8 to 23.7 days between colonies (Table 1). The mean age at onset of foraging was higher closer to winter, which is expected as bees reduce foraging in winter. The age at onset of foraging was similar between hives of the same location and period (Figure 3a).

### Number of flights

Across all colonies, bees on average performed 2.07–9.68 orientation flights and 11.65–48.64 foraging flights during their lifetime (Table 3). Bees in Hobart performed fewer orientation flights than bees in Sydney; however, the number of foraging flights was similar between locations in relation to the season (Figure 3b). This suggests Hobart bees required fewer orientation flights to practice flying or orientate back to the nest. Bees observed during colder months performed fewer foraging flights, likely due to weather conditions (Figure 3b).

### Flight duration

On average, bees spent between 4.35 and 6.67 min undertaking orientation flights, while spending between 23.02 and 64.39 min per foraging flight across colonies

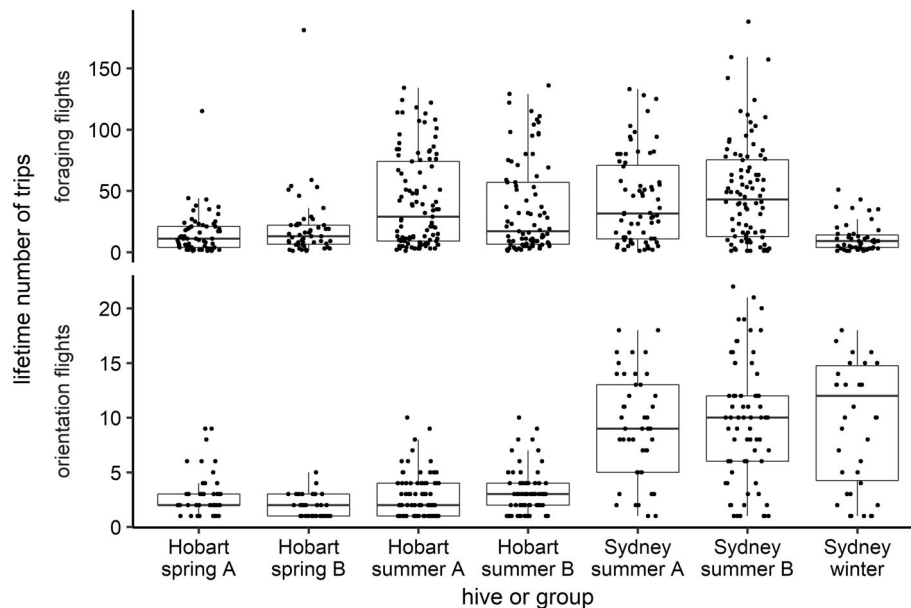
**TABLE 3** Flight parameters per hive (mean  $\pm$  SD). More bees are detected performing foraging flights than orientation flights because some bees are detected to start foraging on the first day they perform orientation flights.

Experiment	Flight type	No. bees	Flight duration (min)	Lifetime flight duration (min)	Lifetime no. flights
Hobart summer A	Foraging	101	64.39 $\pm$ 21.05	3146.99 $\pm$ 2833.89	47.29 $\pm$ 39.95
Hobart summer A	Orientation	83	4.35 $\pm$ 2.65	12 $\pm$ 8.77	2.95 $\pm$ 2.02
Hobart summer B	Foraging	83	59.6 $\pm$ 20.63	2860.38 $\pm$ 2735.68	45.86 $\pm$ 39.03
Hobart summer B	Orientation	68	4.62 $\pm$ 2.72	13.53 $\pm$ 9.04	3.14 $\pm$ 2.07
Hobart spring A	Foraging	63	51.18 $\pm$ 31.56	630.66 $\pm$ 480.96	13.95 $\pm$ 11.38
Hobart spring A	Orientation	41	6.3 $\pm$ 2.05	19.9 $\pm$ 15.38	3.31 $\pm$ 2.41
Hobart spring B	Foraging	51	46.3 $\pm$ 28.73	804.03 $\pm$ 648.45	24.05 $\pm$ 38.71
Hobart spring B	Orientation	36	6.37 $\pm$ 3.28	12.91 $\pm$ 7.35	2.07 $\pm$ 1
Sydney summer A	Foraging	68	23.02 $\pm$ 11.29	1169.8 $\pm$ 1246	42.6 $\pm$ 36.1
Sydney summer A	Orientation	44	5.03 $\pm$ 2.4	39.68 $\pm$ 18.91	9.09 $\pm$ 4.81
Sydney summer B	Foraging	92	34.05 $\pm$ 21.44	1648.27 $\pm$ 1585.72	48.64 $\pm$ 41.02
Sydney summer B	Orientation	69	5.05 $\pm$ 2.6	39.81 $\pm$ 18.48	9.68 $\pm$ 5.53
Sydney winter (pooled)	Foraging	48	32.9 $\pm$ 29.61	373.49 $\pm$ 573.26	11.65 $\pm$ 12.3
Sydney winter (pooled)	Orientation	33	6.67 $\pm$ 4.48	41.44 $\pm$ 21.65	8.82 $\pm$ 5.65



**TABLE 4** Average  $\pm$  standard error and median survival time since tagging with 95% confidence intervals per hive

Hive	<i>n</i>	Mean survival (days)	Median survival (days)
Hobart summer A	112	32.89 $\pm$ 1	32.60 [29.72; 35.69]
Hobart summer B	89	24.36 $\pm$ 0.97	21.63 [18.75; 26.71]
Hobart spring A	80	29.34 $\pm$ 1.4	28.59 [27.59; 30.71]
Hobart spring B	59	28.73 $\pm$ 0.97	29.67 [27.62; 30.73]
Sydney summer A	110	13.22 $\pm$ 0.82	10.56 [8.63; 13.54]
Sydney summer B	141	15.23 $\pm$ 0.81	14.47 [10.7; 16.66]
Sydney winter (pooled)	129	17.48 $\pm$ 1.16	11.55 [9.56; 14.5]



**FIGURE 3** Box and whiskers plots: Thick black lines represent the medians, boxes extend from the first to the third quartile, and whiskers extend to 1.5 $\times$  the interquartile distance. (a) Bees started foraging later during winter and spring. (b) Bees observed in colder months performed fewer foraging flights. Bees in Hobart performed fewer orientation flights, although the number of foraging flights was similar between locations for equivalent seasons. (c) Average flight durations were greater in the Hobart summer dataset. (d) The total time spent foraging was greatest for bees foraging in warmer months. Bees in Hobart spent more time outside in their lifetime even though they performed a similar amount of foraging trips to the bees in Sydney.

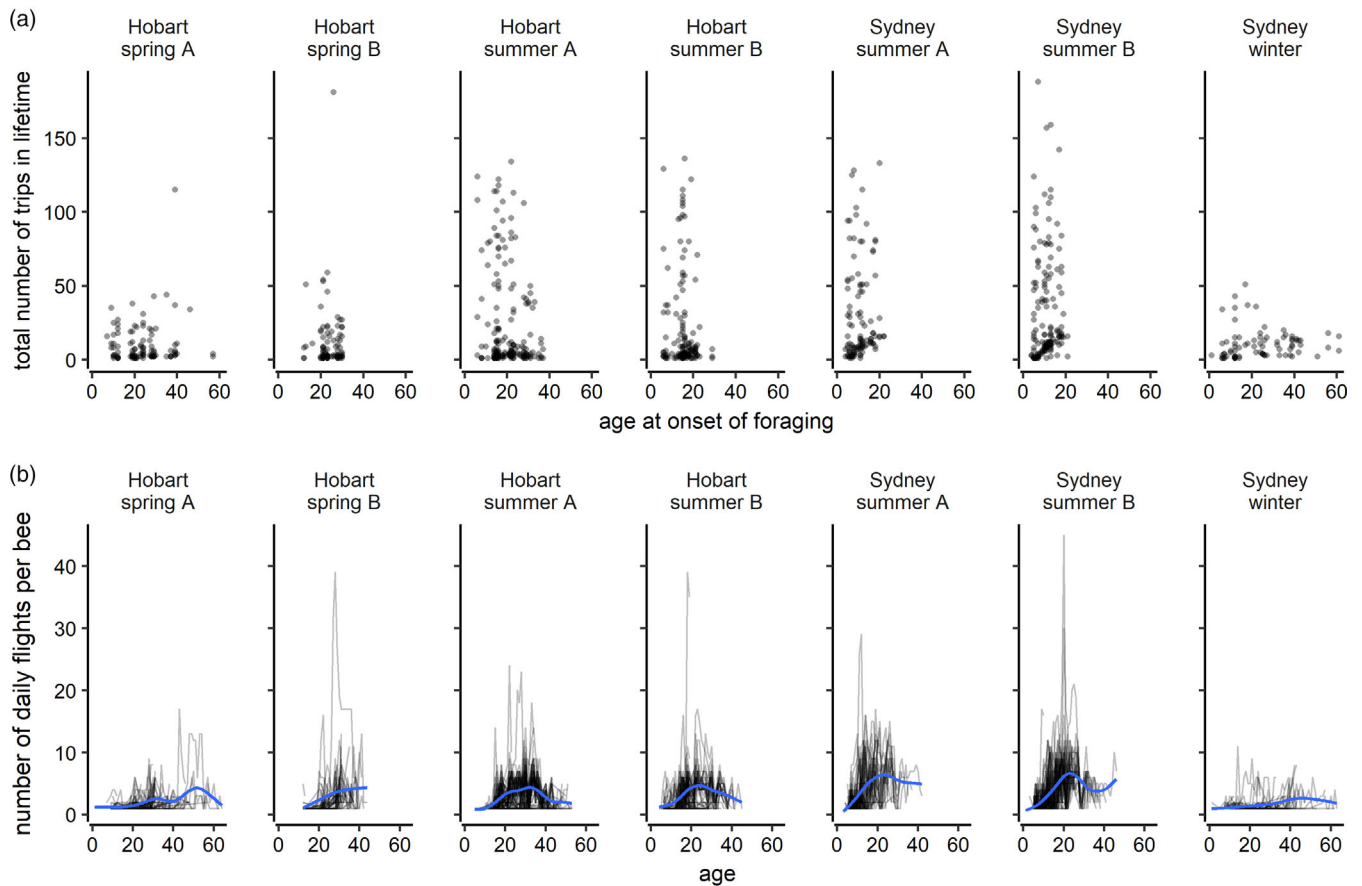
(Table 3). Bees in colder months spent more time on average performing orientation flights than bees in warmer months (Figure 3c). There were no consistent patterns across seasons or locations for the average foraging flight duration, although bees in the Hobart summer dataset performed the longest flights on average (Table 3, Figure 3c).

On average, bees spent a cumulative total of 12.00–41.44 min orienting and of 373.49–3146.99 min foraging in their lifetime across colonies (Table 3). Bees in Sydney spent more time orienting than bees in Hobart (Figure 3c) due to the greater total number of orientation flights undertaken (Figure 3b). The average flight duration was similar between all colonies (Figure 3c). Bees in

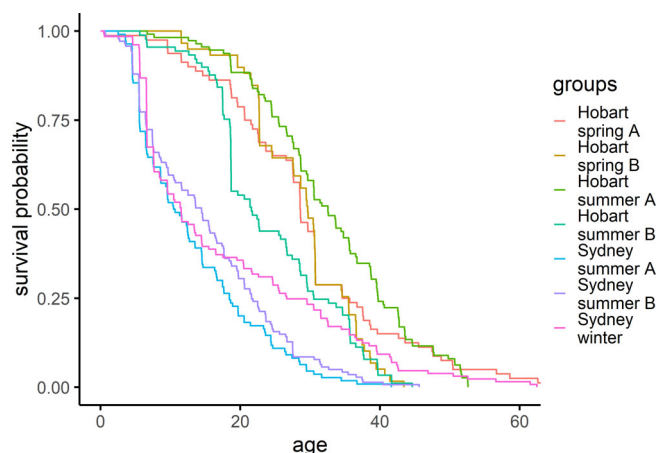
the Hobart summer datasets spent the most time foraging outside the colony (Figure 3c). Overall, bees from warmer seasons spent more time foraging than bees from colder seasons (Table 3, Figure 3d).

### Effect of age on the number of flights

The number of daily flights increased with age (Figure 4), reflecting the increase in number of daily flights after the orientation phase. This number then declined, possibly as an effect of aging. This trend was more prominent for bees observed in warmer months, as fewer flights are undertaken in the colder months (Figure 4).



**FIGURE 4** (a) Total number of orientation and foraging trips in lifetime as a function of the age at onset of foraging in bees that have transitioned to foraging. (b) Number of daily trips performed by each bee as a function of age in bees that have transitioned to foraging. Blue lines represent Loess smoothed conditional means. Bees generally perform between 0 and 10 trips per day. Bees observed in warmer months performed the most trips when they reached about 25 days old regardless of location after which it decreased. This trend was less clear for bees foraging during colder months.



**FIGURE 5** Kaplan–Meier survival curves. Mortality differed between locations (see Table 4 for confidence intervals). Experiments in Sydney used Invengo tags while experiments in Hobart used Murata tags.

## Survival

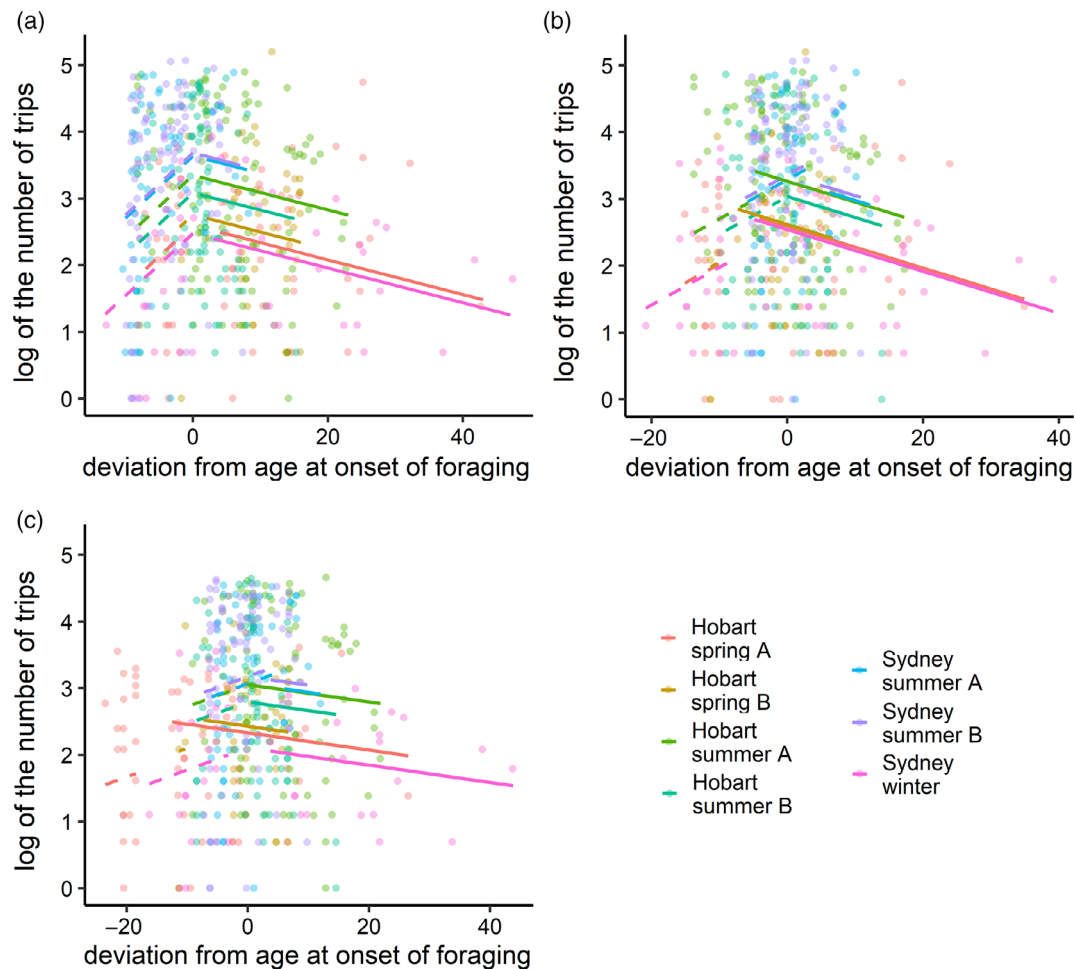
Overall bees in Sydney died faster than bees in Hobart (Table 4, Figure 5). Bees observed in winter in Sydney were

longer lived than summer bees, but in Hobart, bees observed in spring did not live longer than summer bees (Table 4, Figure 5; see also <https://doi.org/10.5061/dryad.83bk3j9s6>).

## Influence of early and late onset of foraging on individual bee performances and survival

Bees that started foraging closer to the three estimated optimal foraging ages performed more trips than bees that started foraging earlier or later. Starting foraging before the estimated optimal age at foraging onset had a stronger negative effect on the number of trips performed than starting to forage after the optimal age (Figure 6, Table 5).

When aging was expressed as the number of days survived since onset of foraging, there were no significant differences between age classes in the 4 to 24 day-old interval, but bees that started foraging outside of this range died at a much faster rate (Figure 7). Bees that started foraging between 12 and 16 days old died at a slower rate than other



**FIGURE 6** Age at onset of foraging and foraging performances. Optimal age set at (a) 14 days from Perry et al. (2015); (b) the mean age at foraging of each colony (see Table 2); (c) the mean age at foraging of elite bees that performed over 25% of the trips (see Table 2; we removed elites data from the analysis and the figure). Foraging earlier than the optimum affected the number of trips performed more than foraging later, but both had a negative effect on the number of trips. Slope estimates of all methods were similar despite optimal age estimates sometimes differing greatly.

**TABLE 5** Effects of early and late onset of foraging on the logarithm of the number of foraging trips performed by bees with three different estimates of optimal age at foraging (log-transformed foraging trips)

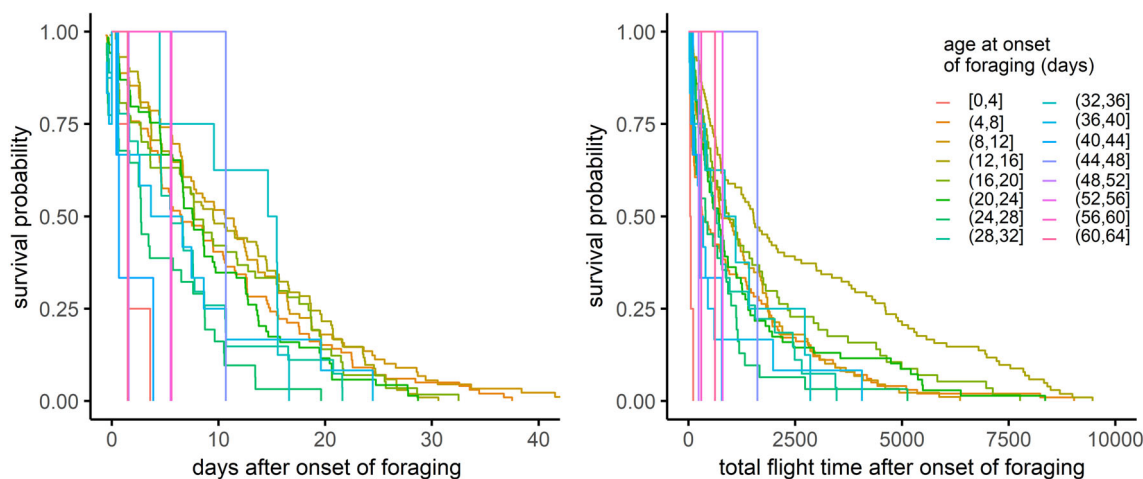
Optimal age estimate	Deviation from optimal onset	Estimate $\pm$ SE	df	t	p
14 days	Early	$0.09 \pm 0.02$	500	4.418	>0.001
14 days	Late	$-0.03 \pm 0.01$	500	-2.895	0.004
Average age at onset	Early	$0.06 \pm 0.01$	484	4.078	>0.001
Average age at onset	Late	$-0.03 \pm 0.01$	496	-2.979	0.003
Average age at onset of elites	Early	$0.03 \pm 0.01$	459	2.744	>0.006
Average age at onset of elites	Late	$-0.01 \pm 0.01$	449	-1.410	0.16

groups when aging was expressed as the total flight time accumulated outside the hive. These were followed by bees that started foraging between 16 and 24 days, and then by bees that started foraging between 4 and 12 days. The few bees that started foraging earlier than 4 days or later than 24 days accumulated very limited flight time (Figure 7).

## DISCUSSION

This article collates RFID data collected from recent and new studies using full-size honey bee colonies. Using the RFID datasets gathered, we explored the generality of assumptions about honey bee forager





**FIGURE 7** Survival of bees after onset of foraging expressed in days (left) or total flight time (right). Data were grouped across all hives and per classes of 4 days to ease representation and meet sample size requirements for survival analyses. Bees that started foraging outside of 12–16 days old (older or younger) died at a faster rate per minute of total flight time (see <https://doi.org/10.5061/dryad.83bk3j9s6>).

development and performance and provide quantified estimates of key parameters of honey bee foraging. We also detail significant advancements in RFID methodology and analytical tools, enabling the collection of large and detailed datasets using full size commercial bee hives in the field.

Previously, the use of RFID for honey bee tracking has been limited by the expense and accuracy of systems. In our methods, we summarize new developments that enhance the utility of RFID for honey bees. We describe an autonomous solar-powered system that can be deployed in remote locations. The RFID readers, antennae, and tags we recommend are readily available, while being substantially cheaper than earlier offerings. We also present the first comparison of the performance of different tags. We describe a new method to deploy an RFID system on a standard commercial honey bee colony that for the first time ensures greater than 90% tag detection accuracy. Our system also solves issues of previous systems affecting bee behavior (reviewed in Odemer, 2022), with the entrance being short, full width, and well ventilated, thus ensuring minimal interference to bee movement, fanning, cleaning, and guarding.

The RFID systems capture an enormous amount of data; hence, it is best to have a standardized method for filtering and analysis of data. Extracting the sequences of entries and exits from the hive is essential for correctly reconstructing patterns of flight activity for each bee. We have provided a workflow and R scripts to optimize the data analysis pathway. These scripts can be utilized for any data collected with the entry–exit event structure, including data collected with QR code systems. Confirming the accuracy of filtering remains one of the limitations of RFID and QR code systems. Visually validating that a bee

performed a full trip is difficult in large bee colonies (Odemer, 2022) and so there is no perfect measure to compare systems. However, with high tag detection accuracy and high bee “funneling” success, there remains little room for incorrect filtering. There is no perfect filter, but the solution we provide is a strong starting point, with potential for widespread application. Extensive comment has been included in the R script attached to help users modify and update it as more knowledge becomes available.

In this study, we chose to remove bees that have never performed foraging trips from the analyses (with the exception of survival analyses). Such data could be analyzed to study bee failure during the orientation phase (Prado et al., 2020). We, however, chose to remove these data from the main manuscript because we observed that some of the large Invengo tags used in the Sydney datasets have prevented some bees from flying or fell off during the orientation phase. The Invengo tags used in Sydney are larger than the Murata tags used in Hobart (Figure 1e) and may be more likely to detach or cause the application of glue to wings. These issues were less severe in the Hobart dataset, which used smaller Murata tags, which we now recommend. Within locations, differences in death rates likely reflected the flight activity of the bees (Prado et al., 2020), with the less active winter bees in Sydney living longer than summer bees, while spring and summer bees in Hobart had more similar dying rates (Figure 5).

Our dataset quantifies variation in bee temporal polyethism. Estimates of the average age at onset of foraging varied from 10-day-old adults in the Sydney summer dataset to 23 day-old adults in the Hobart spring dataset. This variation in the age at onset of foraging was likely due to differences in seasons and food abundance

between experiments. Classic studies proposed bees began foraging between 14 and 21 days of age as adults (Capaldi & Dyer, 1999), and across our datasets, the modal age of foraging onset was 14.75 days old, which was slightly lower than Prado et al. (2020).

The poor performance and earlier mortality of bees that commenced foraging at a young age also suggests that the age of foraging onset is a key parameter influencing lifetime forager performance (Henry et al., 2015; Perry et al., 2015; Prado et al., 2020; Scofield & Mattila, 2015; Søvik et al., 2015). Across our datasets, we also saw evidence for an optimal age at foraging onset. Irrespective of how we estimated the optimal foraging age, bees that commenced foraging older or younger completed fewer foraging trips (Table 1, Figure 3). Bees that started foraging earlier than 12–16 days old died at a faster rate when considering the total time spent flying outside, but not if considering age in days. Bees that started foraging later died at a faster rate both in terms of days and total flight time (Figure 7).

This supports a key assumption for modeling honey bee colony failure. A sustained stress that causes precocious foraging onset or early death of existing foragers can push colonies into a destructive positive feedback cycle. Bees that commence foraging precociously will perform poorly and die prematurely, which can compound the stress on a hive and place the colony at risk of catastrophic population destabilization.

Orientation flights were also reliably detected in our datasets and could be differentiated from foraging based on a simple individual threshold of total time spent outside on each day. The transition from orientation flight to foraging onset is pronounced (Figure 2). Orientation flights were few and of short duration (typically less than 20 flights shorter than 5 min; Figure 3). These parameters confirm previous estimates based on a few bees (Capaldi et al., 2000; Menzel et al., 2005). The parameters of the orientation phase differed between our datasets, which could reflect difficulty to learn the hive's location. It will be interesting in future to explore whether the number and duration of orientation flights relate to visual landmarks available to young bees.

Bees typically performed less than 150 foraging flights in their lifetime, undertaking 33 trips of 44 min on average (Figure 3). The average flight duration differed between locations (Figure 3), suggesting differences in navigation difficulty, distance to the floral resources, or time necessary to collect the same amount of nectar or pollen. Future research could investigate which types of crops and landscapes reduce the length of foraging trips.

The use of RFID and QR code systems to measure the life history traits of honey bees has been limited by the lack of reproducible methods. Here, we have presented our contribution to the development of more

standardized RFID systems by providing methods to separate honey bee traffic, to operate RFID systems, and to deal with the large amount of data that RFID systems generate. We hope this might encourage the use of RFID systems to generate large datasets on the flight performances, survival, and flight ontogeny of bees worldwide. As more datasets accumulate, accurate stochastic modeling of bee colonies will become possible. As a starting point, we here demonstrate how useful measures of life history traits can be obtained.

## AUTHOR CONTRIBUTIONS

Théotime Colin, Andrew B. Barron, Ryan J. Warren, Stephen R. Quarrell, and Geoff R. Allen designed the experiment and the methodology; Théotime Colin and Ryan J. Warren collected field data; and Théotime Colin, Andrew B. Barron, Ryan J. Warren, Stephen R. Quarrell, and Geoff R. Allen wrote the manuscript.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.


## DATA AVAILABILITY STATEMENT

Data (Colin et al., 2022), code, hive entrance design, demonstration video, photos, and 3D models are available from Dryad: <https://doi.org/10.5061/dryad.83bk3j9s6>.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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