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RESEARCH

Honeybee egg size is linked to land use and predicts worker foraging performance

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Abstract
Humans have changed the nutritional landscape available to bees, increasing the risk of nutritional stress and health challenges. Honey bee (*Apis mellifera*) queens are known to increase worker egg size during times of nutritional stress, suggesting that land use may affect honey bee egg size. Furthermore, it is currently unknown whether a change in egg size has downstream consequences for adult workers. We tested if egg size varies between rural and urban areas in south-west England. Egg size in rural areas was significantly larger, indicating nutritional differences between the two land use types. Increased colony weight, suggesting increased food stores, were associated with smaller egg sizes. Experimentally inducing queens to lay larger eggs by colony splitting and then using radio-frequency identification (RFID) technology, we found that bees from larger eggs performed 23.8% more foraging trips. However, there was no significant effect of egg size on bee body size or lifespan. These findings suggest that egg size may influence foraging activity in honey bee colonies without impacting other important adult worker traits. Future research should address the mechanisms linking egg size to worker behaviour under varying environmental conditions.

Keywords Honeybee · Land use change · Colony health · Nutrition · Egg size · Foraging behaviour

Introduction

Humans benefit from insect pollination, which supports the production of food, especially nutrient-rich fruits and vegetables (Klein et al. 2007). However, a paradox arises where human activities, such as land use change, cause pollinators to struggle to find enough food for their own maintenance (Goulson et al. 2015; I'Anson Price et al. 2019; Naug 2009; Potts et al. 2010). Urban areas, for example, are often associated with reduced bee diversity (Liang et al. 2023). Allotments and suburban gardens, however, can function as "hot-spots" for pollinators (Baldock et al. 2015, 2019; Timberlake et al. 2024a) because they host diverse floral resources and provide consistent access to pollen and nectar throughout the foraging season (Tew et al. 2021, 2022). In comparison, the "boom and bust" cycles in intensively farmed landscapes provide surplus floral resources at limited moments throughout the year and nutritional gaps during other periods (Couvillon et al. 2014a; Goulson et al. 2015; Timberlake et al. 2019). In addition, intensively farmed areas typically produce a low number of pollen varieties and offer limited nutrition for visiting pollinators (Goulson et al. 2015). Thus, bee populations may receive better nutrition in some urban areas with access to essential nutrients which are vital for health and survival (Branchiccela et al. 2019; Requier et al. 2017; Baldock et al. 2019; Tew et al. 2022).

The Western honey bee (*Apis mellifera*) is a particularly important pollinator of wild and agricultural plants in many regions (Hung et al. 2018) and nutrition is a key factor affecting the life history of individuals and overall colony function (DeGrandi-Hoffman et al. 2010; Huang and Giray 2012). Pollen shortages are linked to reduced

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brood production, increased parasite and viral loads, and decreased rates of colony survival over winter (Branchiccela et al. 2019; DeGrandi-Hoffman et al. 2010; Requier et al. 2017). Workers in honey-starved colonies experience accelerated rates of maturation to become foragers at a younger age (Schulz et al. 1998), which is associated with reduced worker longevity and health over the long term (Guzman-Novoa et al., 1994; Rueppell et al. 2007). In response, bees from honey-starved colonies show increases in health-related gene expression (Wu et al. 2024).

One key-life history trait affected by nutrition is egg size. A lack of food stores inside the hive or a small colony size induces queens to lay larger eggs (Amiri et al. 2020a; Han et al. 2022). Queens can lay up to 2,000 eggs each day (Laidlaw & Page, 1997) and due to the costs of reproduction, it is expected that egg size is under strong selection, especially when colonies are nutritionally strained. Egg size manipulations may serve as a mechanism for adaptive maternal effects because honey bee egg size likely reflects offspring provisioning and resource allocation (Amiri et al. 2020a; Fox et al. 1997). Enlarging eggs may be a short-term response that can only be maintained for a few days or weeks, as resources are finite: older queens who may have had their resources depleted produce eggs that are on average 30% smaller than those from young queens (Al-Lawati and Bienefeld 2009). Larger egg size is associated with enhanced offspring survival in many oviparous species, for example in birds (Krist 2011; Griesser et al. 2023; Schwagmeyer and Mock 2008), lizards (Sinervo and Doughty 1996) and fish (Einum and Fleming 1999). The mechanisms through which larger eggs improve offspring fitness include enhanced growth, resistance to starvation, and better predator avoidance (Segers and Taborsky 2011). In honey bees, larger eggs were more likely to survive larval and pupal development and reach adulthood (Amiri et al. 2020a). Theoretically, mothers should adjust reproductive investment according to the predicted environment offspring will grow up in (Marshall and Uller 2007).

In honey bees, queens are able to perceive colony size and manipulate egg size in as little as two days after colonies have been split experimentally (Amiri et al. 2020a), possibly by assessing contact rates with workers, levels of pheromones (Ma et al. 2018; Pankiw 2004; Trhlin and Rajchard 2011) and potentially even temperature (Seeley 1989) where increasing or decreasing the number of heat-emitting individuals may affect temperature gradients (Smith et al. 2017). Large egg size could result in large worker body size, which has been linked to foraging efficiency, immune function, and overall fitness in some bees (Spaethe and Weidenmüller 2002; Ramalho et al. 1998; Veiga et al. 2013). A recent study has investigated the link between egg size and worker size in honeybees. Han et al. (2023) show that worker size may be mediated by both egg size and colony size, where bees from small eggs cross-fostered into large colonies can catch up with the larvae from large eggs, but remained smaller when reared in small colonies. Compensatory growth may occur through the action of enhanced nursing behaviour where resources are sufficient.

Here, we studied the relationship between land use, nutritional state and honey bee egg size by comparing egg size in predominantly rural *versus* predominantly urban environments. We then experimentally manipulated egg size and explored whether egg size predicts worker size, foraging behaviour and lifespan using radio frequency identification (RFID) data. We predicted that queens in rural environments lay larger eggs due to challenging foraging conditions and that workers from larger eggs are larger and will exhibit greater foraging activity, which could alleviate nutritional strain on the colony.

Methods

Experiment 1: does land use predict egg size?

Site selection

The study was performed from August to October 2022 in the southwest of England. ArcGIS (Version 10.7.1, Esri) (Marston et al. 2022) was used for land use composition analysis, which allowed us to select six sites for the study (Figs. 1 and 2). A 1.5 km radius was drawn around each selected hive site and the area inside was described by land use types represented as a percentage. Honey bees collect most resources within 1.5 km during the study period (Couvillon et al. 2014b; Samuelson et al. 2022). Categories of land use were as follows: “Suburban”; “Urban”; “Neutral grassland”; “Improved grassland”; “Arable & Horticulture”; “Coniferous woodland”; and “Deciduous woodland” (Marston et al. 2022).

The three sites composed of > 50% “Suburban” and “Urban” land were categorized as “Urban” (the cities of Bristol, Bath and Swindon), while the remaining three sites were classified as “Rural” (Table S1 in Online Resource 1; Fig. 2). “Urban” sites were on average 12.8% ± 8.89 (mean % ± SD) urban and 67.9% ± 14.05 “Suburban” (Fig. 1). “Rural” sites were dominated by improved grassland, comprising on average 61% ± 7.54. The second most dominant land-type in “Rural” areas was “Arable and Horticulture” (15% ± 9.12).

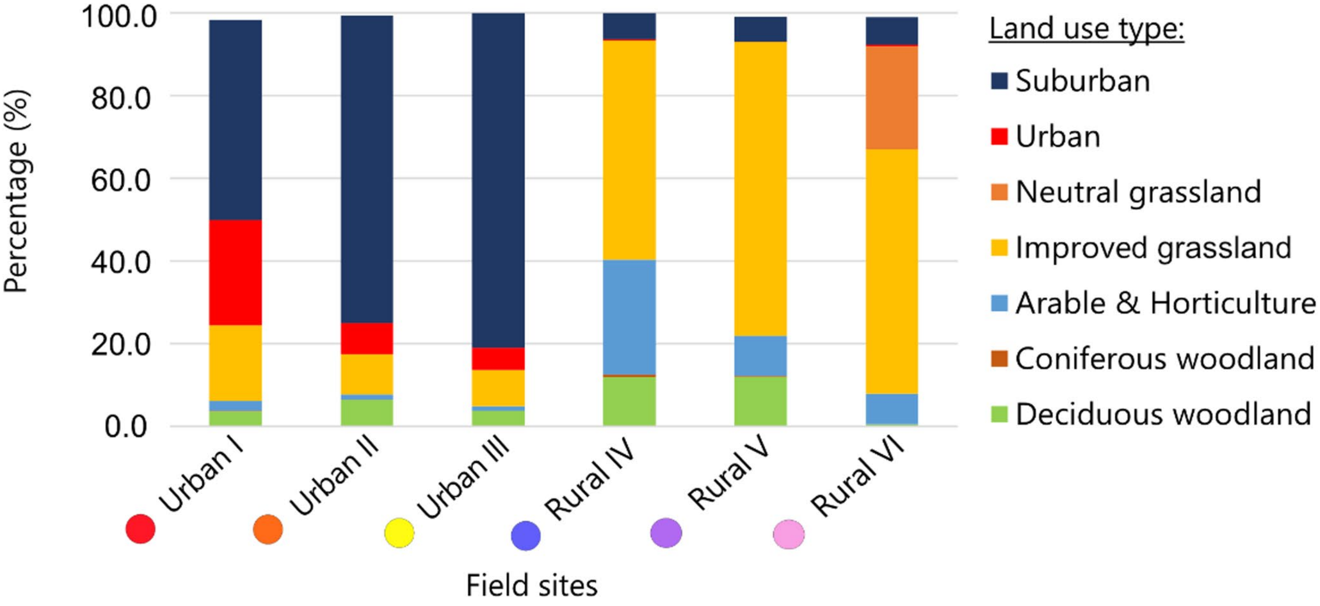

Fig. 1 Landscape composition surrounding the six field sites. A 1.5 km radius was drawn around each hive and the proportional coverage of each land use type within the circle boundary is displayed as a percentage (ArcGIS, 2022)

Egg collection and measurement

To measure egg size, we collected eggs (aged 0–3 days) from six *Apis mellifera* colonies, with one hive located at each site (Fig. 2). Colonies originated from an apiary near the University of Bristol and were brought to the different sites several weeks before egg collection. Colonies had approximately 20,000–40,000 honey bees and were maintained in identical Langstroth hives made of 2 medium boxes, each containing 9 frames. All hives were inspected every 18 days in a standardised way. Queens had typical queen age (the majority were less than a year old, a few queens were 1–3 years of age), predominantly *A. mellifera mellifera* and queens were of mixed relatedness (relatedness was not controlled or tracked in the apiary).

One frame per hive was used for egg collection. A sample of comb with eggs was extracted using a circular cookie cutter (ø=6.50 cm, A=33.18 cm^2) and was then transported back to the lab using a plastic sealed container to maintain humidity. Eggs were extracted using a grafting tool and deposited long-side down and photographed using a ZEISS Axiocam 208 colour lab scope (Fig. S1 in Online Resource 2). Pictures of eggs were processed using ImageJ (Schindelin et al. 2012). Egg planar area (mm^2) was selected as the primary proxy for egg size as it best represented honey bee egg shape (Amiri et al. 2020b).

Colony weight

Day-to-day colony weight loss indicates that the consumption of food exceeds supply, while weight gain indicates favourable foraging conditions (l'Anson Price et al. 2019; Seeley and Visscher 1985). We expected to see larger eggs in colonies that have experienced a recent decline in colony weight. Therefore, we monitored colony weight changes 14 days prior to egg sampling. Hives were placed on BeeWatch hive scales (±20 g accuracy) and their weight was recorded at 12.00AM (midnight) when all forager bees were inside the hive (Table S1 in Online Resource 1).

Experiment 2: egg size consequences on worker size and foraging performance

Behavioural observations were done at the University of Bristol Vet School in Langford (51.3469° N, 2.7783° W).

To investigate how egg size impacts worker size and behaviour, we experimentally induced egg size variation by manipulating the size of the colony as in Amiri et al. (2020a); Han et al. (2022). Full-sized colonies containing ~ 30,000–50,000 bees were inspected prior to the experiment and those with sufficient food and brood were used. We used a paired design approach: two colonies of similar size were paired, one was randomly allocated as *treatment*, the other used as *control*. To create a *treatment* colony, two frames with workers, brood, food stores and the queen (~ 3,000–5,000 bees) were removed from a full-sized hive and moved into a hive box with an additional empty frame between the two full frames to provide comb space for the queen to lay eggs. We left the queen for five days to lay eggs. The *control* colony was left whole (Fig. 3). We tested three pairs of colonies.

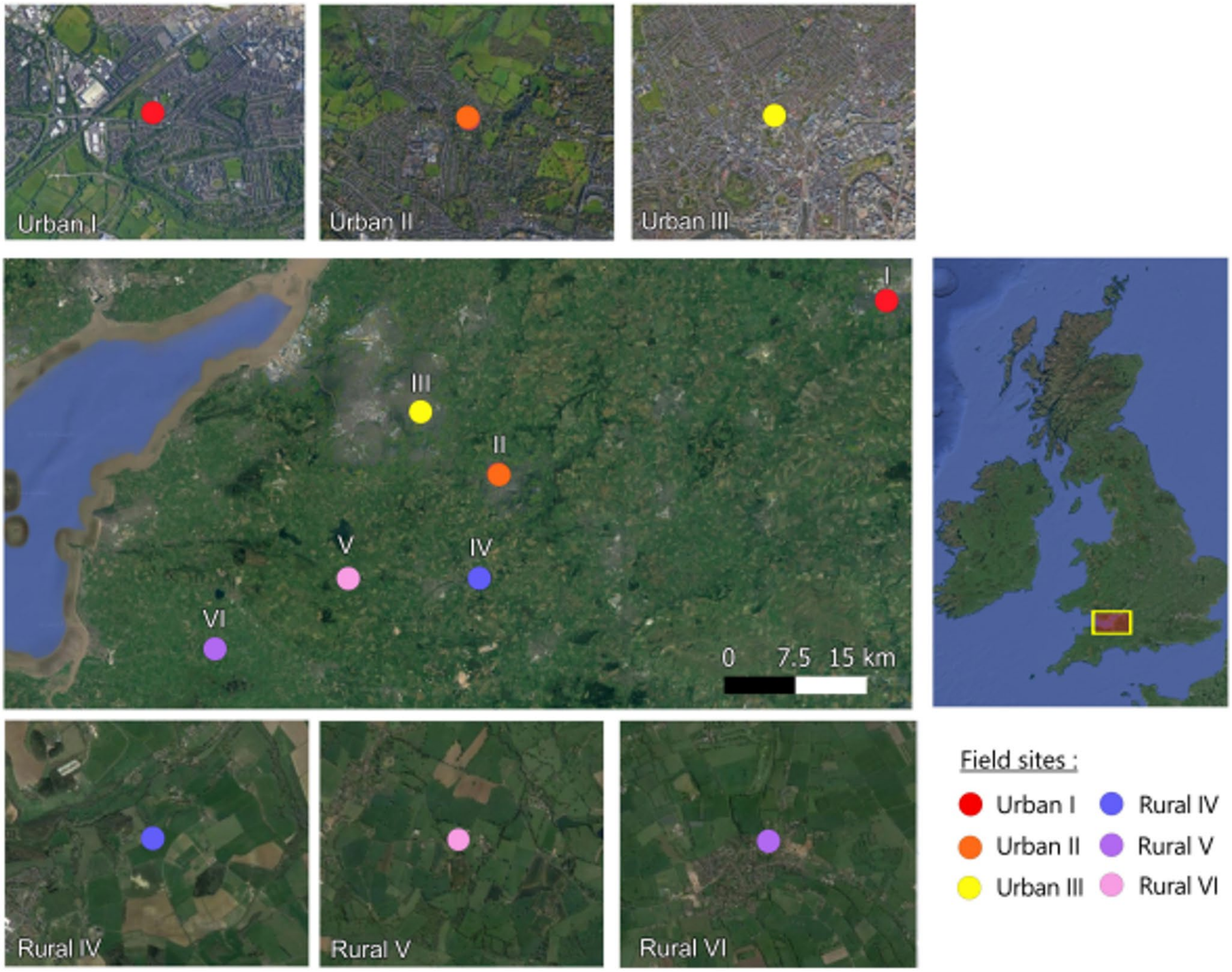

Fig. 2 Map of the six sites where honeybee eggs were extracted from six colonies. Top row and bottom row images show closer aerial view from Google Satellite/Terrain databases accessed in 2023 for a visual representation of the land use present at sites as of 2023. A scale and legend are inlaid, including an overlay map to show the location of the Southwest within the UK

Bees spend three days as an egg, therefore we removed eggs from colonies five days after splitting to ensure eggs were laid post-splitting event. Egg frames from both *control* and *treatment* hives were moved into a third, common garden colony to standardize hive conditions and the feeding of the larvae from nurse bees. To confirm that splitting caused queens to lay larger eggs, a sample of ~10 eggs per colony were taken on day five for measuring as described above. After 15 days in the common garden hive (20 days post-splitting), bees were nearly ready to emerge and the two frames containing capped brood (1 *treatment* and 1 *control* frame) were removed and placed in separate Correx 6-frame Nuc boxes in an incubator (Thermo Scientific Heratherm Incubator 18738), where they were kept at 34 °C (Fig. 3; Box 2). Worker bees take ~21 days between oviposition and emergence (Winston 1991); on days 23, 24 and 25 after splitting, our focal honey bee brood emerged. To investigate how egg size correlates with bee size and behaviour, a sample of approximately 10 newly emerged worker bees were collected and stored in a −20 °C freezer for measurement. Thus, while we were unable to measure the egg and worker size of the same individual, we used two separate samples from the same frame to correlate average egg size with individual worker size. Prior measurements demonstrated that egg size is consistent within the same frame (Amiri et al. 2020a).

Measuring worker size: head width and wing length

The heads and wings from newly emerged bees were removed and placed next to each other on graph paper. Photos were taken and analysed as described for the egg measuring. Two measurements were taken for each bee: head

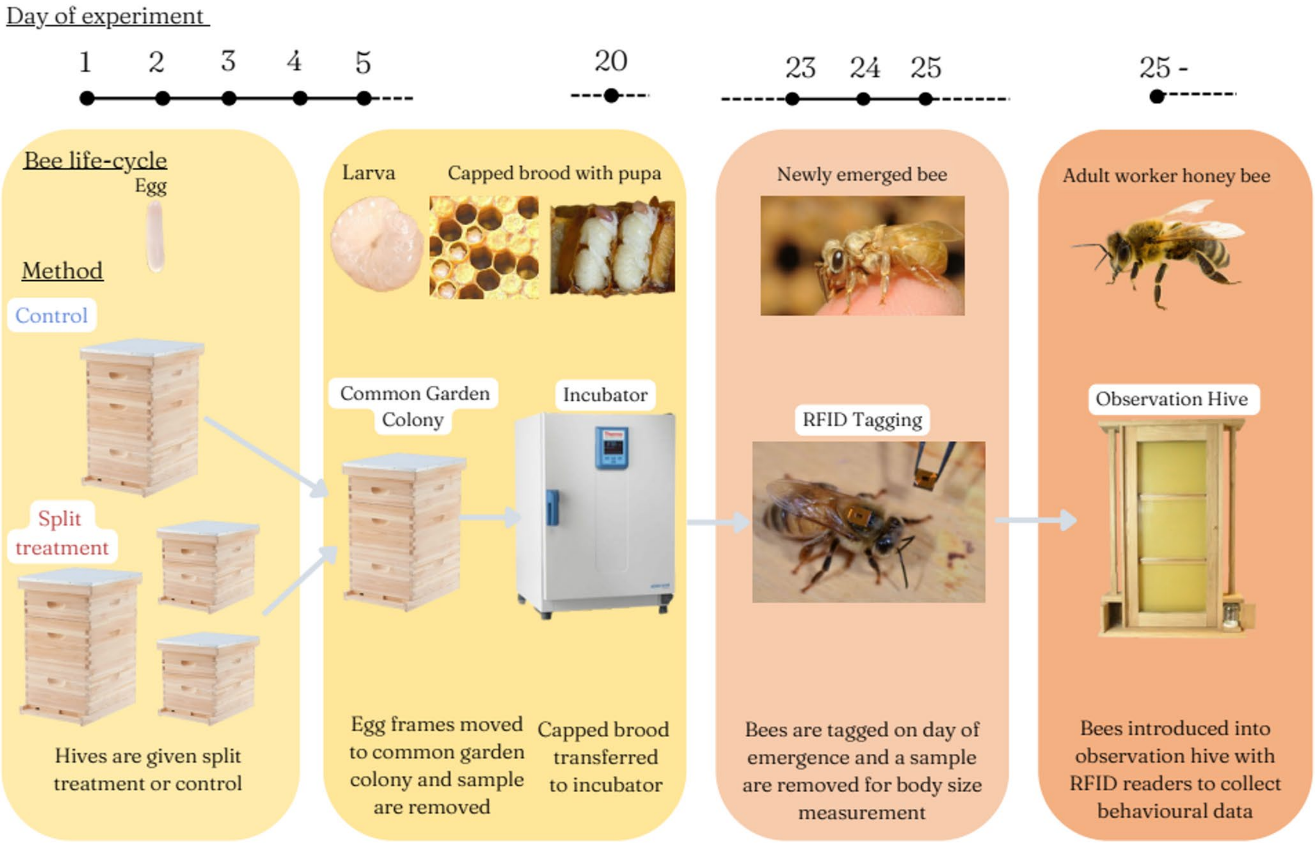

Fig. 3 Method and time schedule for colony splitting to generate egg size variation, measuring bee size and recording behaviour, with a timeline in days across the top beginning at day 1 when the colonies were split and ending with introduction into the observation hive. Eggs selected for study were laid on days 2–5. The cycle was repeated with six colonies in a paired design

width (distance between the distal surfaces of the eyes, measured dorsally) and wing length (distance from where wing cells begin near the body to the distal edge of the wing). Head width is commonly used to estimate body size in bees (e.g. Kamm 1974; Sauthier et al. 2017; Wu et al. 2025). Since head width and wing length may not always scale isometrically in bees (Grüter et al. 2012), both head width and wing length were recorded as a proxy of worker bee size in this experiment.

Measurement of foraging performance using radio-frequency identification (RFID).

To record the foraging activity and lifespan of bees from different egg sizes and treatments, newly emerged bees were transferred to an observation hive monitored by a radio-frequency identification (RFID) system ("Maja Bundle", Microsensys GmbH, Erfurt, Germany). Focal bees from all hives were studied in the same three-frame observation hive to standardise hive conditions. The observation hive was set up a few weeks before the introduction of the focal bees and contained 2,000–4,000 workers, brood, food stores and a naturally mated queen. The observation hive was kept inside a shed and was fitted with two radio-frequency identification (RFID) readers (MAJA reader module 4.1) used in sequence to record departure and arrival times of tagged bees. A piece of clear plastic tubing created a walkway for bees to move from the hive to the exit of the shed passing the RFID readers along the way.

Bees from *treatment* and *control* frames were tagged within 24 h of emergence. Using a queen-marking device, bees were given a spot of acrylic colour on their abdomen to denote *treatment* or *control*. An RFID tag (mic3-Tag 16 K, Microsensys GmbH, Erfurt, Germany) was attached to the bee's thorax using transparent nail-varnish. Tagged bees were temporarily stored in a plastic container and were then introduced into the observation hive in batches. Bees from different pairs were introduced sequentially. RFID recording lasted for 14 weeks, exceeding the typical lifespan of temperate honey bees during the active foraging season (3–6 weeks, Winston 1991). By the end of RFID recordings, only few tagged bees were left in the observation hive.

The following foraging behaviours were analysed: the number of foraging trips per bee, duration of foraging trips, age at first foraging, age at last foraging trip, foraging lifespan and total lifespan. The *Track-a-Forager* program was used to analyse and filter the raw data (Van Geystelen et al. 2016). Due to a technical problem with the RFID raw data, we were unable to use the RFID data from the last colony pair, leaving us with RFID data from four hives.

We removed trips shorter than 3 min because they are unlikely to represent foraging trips (they may have represented short orientation flights), based on knowledge of foraging trip durations (Park 1926; Peng et al. 2021; Van der Steen 2015). Trips over 8 h (28,800 s) were discarded as they were unlikely to represent foraging trips, however, they may occur when honeybees fail to return before temperatures decrease and bees stay outside of the hive overnight (Colin et al. 2022).

Data analysis

All statistical analyses were performed in R 4.2.1 (R Development Core Team 2008). Data was summarised as mean ± standard deviation. General linear models and linear mixed effect models (LMEs) using packages “lme4” and “lmerTest” (Bates et al. 2015) were used. In the latter case, colony ID or bee ID were used as a random factor to control for the non-independence of data from the same colony or the same bee (Zuur et al. 2009). Model residuals were checked using the package “DHARMa”. If transformations were necessary to achieve a normal distribution of residuals and to stabilise the variance we used either a log-transformation, or the box-cox transformation using the package “MASS” (Crawley 2012).

Experiment 1: does land use predict egg size?

Linear mixed-effects models (LMEs) were used to investigate if the main land use categories and colony weight change or their interaction predicted egg sizes. Colony ID was included as a random effect. An LME was run with overall changes to colony weight during the 14 days before egg collection, referred to as cumulative weight change (CWC) as our predictor variable, egg size as the response variable and colony ID included as a random effect. Subsequently, we used likelihood ratio tests (LRTs) to examine potential interactions between land use types and cumulative weight change (CWC) on our response variable egg size. Since CWC significantly influenced egg size, we used a linear model (LM) to explore if any land use type predicted CWC.

Experiment 2: egg size manipulation and downstream consequences on worker size and behaviour.

An LME was used to test for differences in egg size, bee head width and wing lengths between *treatment* and *control* colonies. Colony was included as a random effect. LMEs were used to test the effect of treatment, egg size, and body size on foraging activity. Foraging activity was measured as foraging trip number, trip duration, total foraging duration, age at onset of foraging and lifespan (based on the last day of foraging activity). Colony ID was included as a random effect. In addition, we investigated the relationship between foraging trip number and trip duration per bee. Our model used trip number as the predictor variable and total trip duration as the response variable, with colony ID as a random effect.

Results

Experiment 1: does land use predict egg size?

We measured 162 eggs, 52 from rural hives and 110 from urban hives (26.16 eggs ± 21.28 per colony). Egg size was significantly larger (+45% in area, +22% in length) in rural than urban hives (Fig. 4) (LME, Length: $F_{1,160}$ = 184.5, $p < 0.001$; Area: $F_{1,160} = 224.8$, $p < 0.001$). Full model specification can be found in Table S3 in Online Resource 1.

Cumulative weight change (CWC) of colonies strongly and negatively predicted egg size (LME: t = −6.028, $p = 0.00359$) (Fig. 5). Given that suburban areas in the Southwest of England are thought to offer good foraging opportunities for bees (Baldock et al. 2019; Tew et al. 2022), we tested whether the percentage of suburban land predicted cumulative weight and but found no effect (LM: t = 1.757, $p = 0.154$) potentially due to a small number of sites used in this study ($N = 6$).

Experiment 2: egg size manipulation and downstream consequences on worker size and behaviour

Overall, 327 eggs were analysed from 6 colonies under two treatments (25.15 eggs ± 18.53 per colony). Eggs from treatment colonies had an average area of 0.525 mm^2 and were significantly (~8%) larger than control eggs which had an average area of 0.487 mm^2 (Figs. 6 and 7; Table S3 in Online Resource 1) (LME: F = 6.952, $p = 0.005$).

A total of 158 newly emerged bees were measured ($N = 74$ *treatment*; $N = 84$ *control*). We found a significant interaction between treatment and egg size on head width (Fig. S3a in Online Resource 2) (LRT = 4.87, $p = 0.027$). When analysing the treatment conditions separately, we found that egg size showed a positive but non-significant relationship with head widths in control conditions ($p = 0.093$), whereas no relationship was found in treatment conditions ($p = 0.648$) (Fig. S3a in Online Resource 2). Treatment significantly and positively affected wing lengths (LRT = 2.31,

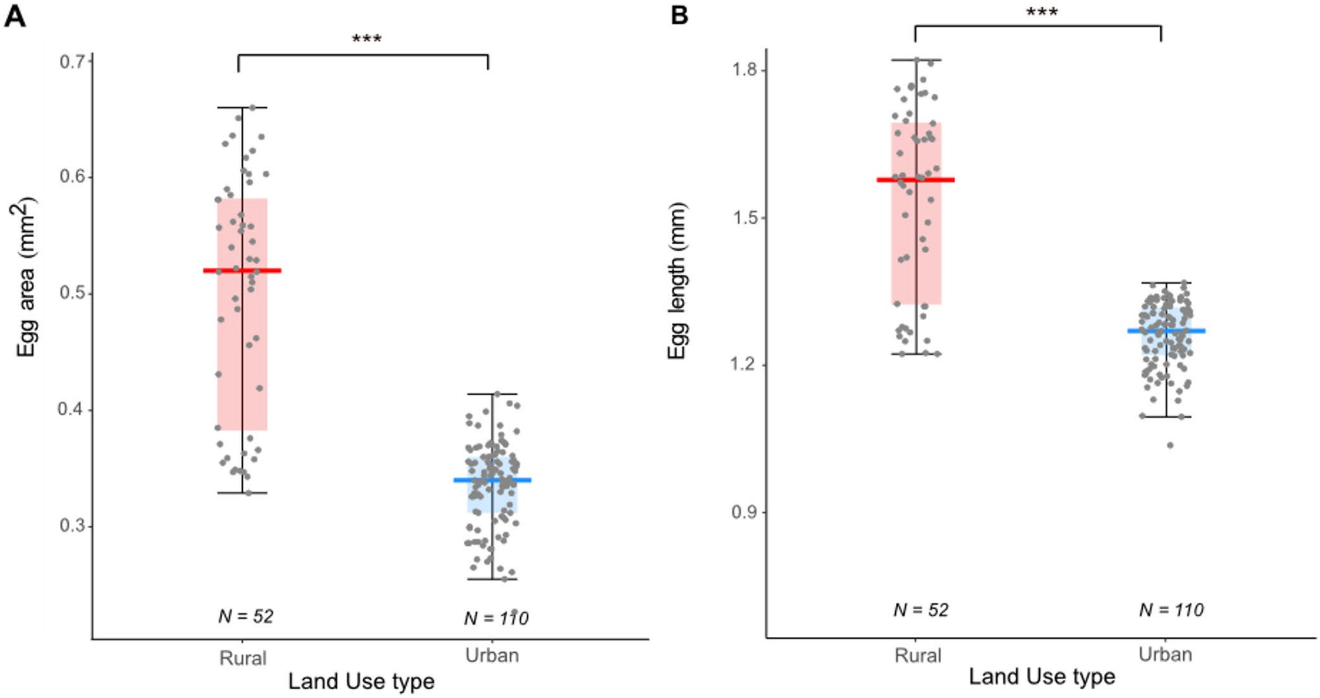

Fig. 4 Egg size differences produced by queens in different land use types. Egg size (mm^2) = egg planar area. **A** Queens in rural colonies produce eggs with a significantly greater planar area than eggs produced in urban colonies (Rural = 0.48 ± 0.05 mm^2; Urban = 0.33 ± 0.0064 mm^2, N = 162). **B** Rural eggs were significantly longer than urban eggs (rural = 1.54 ± 0.03 mm; Urban = 1.26 ± 0.0064 mm, N = 162). Plots show the median (thick line), the 25% and 75% quartile ranges (shaded boxes) and individual data points (grey dots). Significance displayed *** = $p < 0.001$

p = 0.022), whereas egg size did not affect wing length (p = 0.062) (Fig. S3b in Online Resource 2; Table S3 in Online Resource 1).

Foraging performance

From the RFID data we identified 235 individual bees (120 treatment bees, 115 control bees), which performed 6,346 foraging trips in total (median = 16 trips/bee, range = 1–132). Raw foraging data can be accessed from repository (DOI https://doi.org/10.5061/dryad.sxksn03g9). The most common trip durations were 5–10 min (Fig. 8A), possibly indicating water collection and trips to blackberry (*Rubus* sp.) and ivy (*Hedera helix*), which were abundant nearby. A small number of bees completed a large proportion of foraging trips: 17% (N = 40) of bees performed 50% of all foraging trips, while 14% of bees (N = 34) performed 50% of the total foraging time. We found a strong positive correlation between the number of trips taken by a forager and the trip duration (LRT = 8.981, $p < 0.001$) (Fig. 8B: $R^2 = 0.47$).

Effect of treatment and egg size on foraging trips

There was a significant effect of treatment on total foraging trip number (LME: t = 2.05, p = 0.041). Bees from treatment colonies undertook ~24% (5.41 trips) more foraging trips on average than bees from control colonies (Fig. 9A). We found that egg size positively affected trip number (t = 2.05, p = 0.041). However, the average duration of trips did not depend on egg size (t = 0.639, p = 0.524). The cumulative foraging time over the entire lifetime was ~21% longer in treatment bees compared to control bees (20.6 ± 2.17 h vs. 17 ± 2.05 h), but this difference was not statistically significant (t = 0.919; p = 0.550), nor was there a significant affect of egg size on total cumulative foraging duration (t = 1.02, p = 0.308, see Table S3 in Online Resource 1).

The age of first foraging (control: 12.8 ± 0.5 days, treatment: 14.3 ± 0.7 days) of the bees was not predicted by treatment (t = −0.713, p = 0.61), nor was it predicted by average colony wing length (t = −0.690, p = 0.62) or egg size (t = 0.801, p = 0.57). Worker lifespan (control: 25.7 ± 1.77 days; treatment: 25 ± 1.49 days; see Table S1) was not predicted by treatment (t = -0.714, p = 0.68), nor egg size (t = 0.742, p = 0.65), nor wing length (t = −0.907, p = 0.58, see Table S1).

Discussion

Our findings from Experiment 1 confirm that egg size variation exists in different land-use types and Experiment 2 suggests that bees from larger eggs performed more foraging

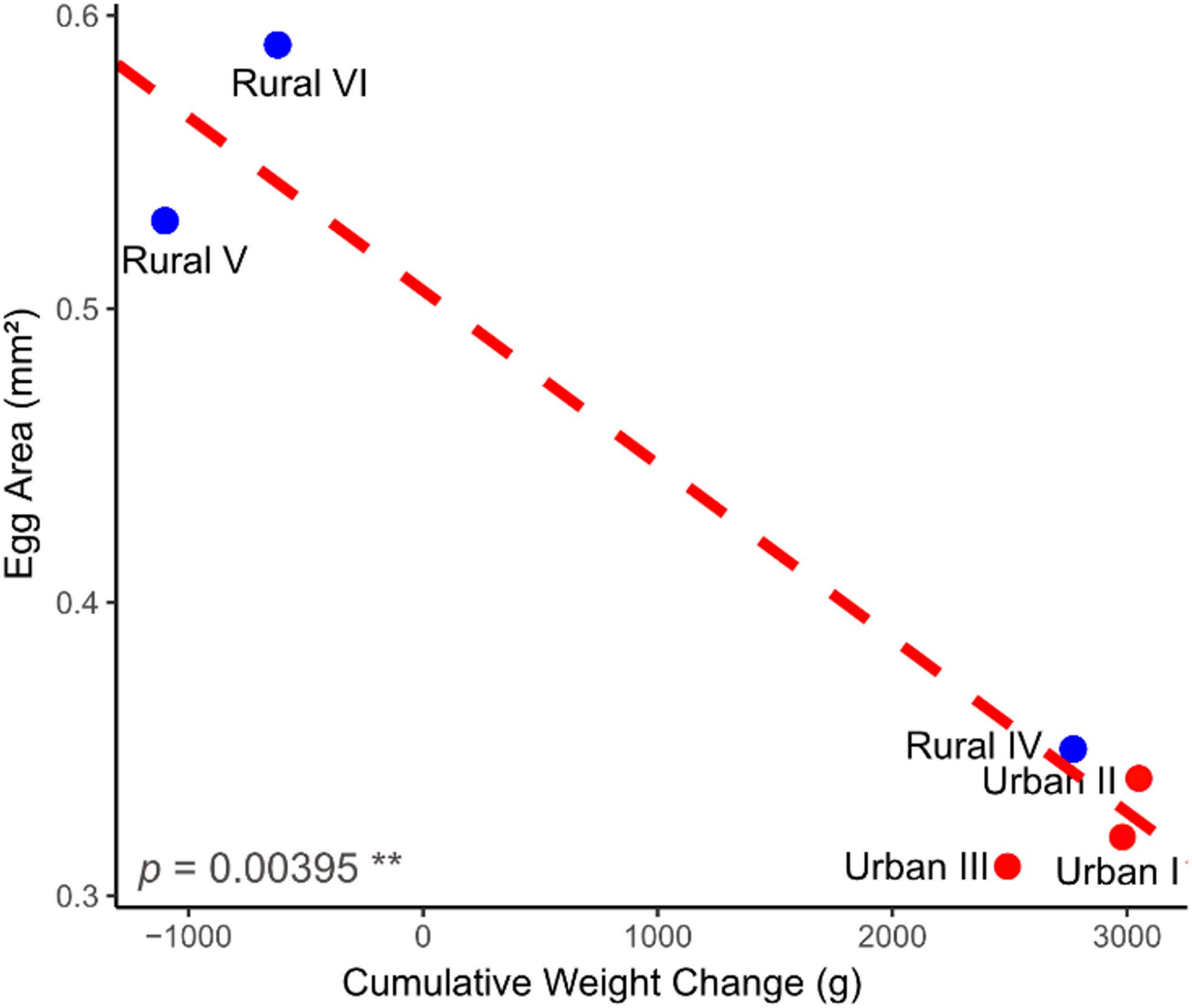

Fig. 5 The relationship between egg size and cumulative colony weight change (CWC). Egg size, measured as planar area (mm^2) changes with CWC across sites

trips, however there was no demonstrated effect on other traits such as lifespan or worker size. In rural areas queens laid 45% larger eggs (Fig. 4), possibly to provision each with more nutrients, hormones, immune factors or other molecular signals when food is scarce. By laying larger eggs that may enhance offspring survival (Amiri et al. 2020a), a queen honey bee might reduce investment in resources and brood care required by nurse bees. Colonies in urban areas may have benefitted from food sources availability in suburban gardens and allotments, potentially reducing the need for larger eggs (Baldock et al. 2019; Tew et al. 2022). Accordingly, queens in colonies losing weight during the 14-day period before egg collection produced larger eggs, while those which gained weight produced smaller eggs (Fig. 5). It should be noted that only six field sites were used for Experiment 1 and measured ~ 26 eggs per colony. For Experiment 2, we measured 158 bees to compare phenotypic traits and only 235 bees were radio-tagged overall. This relatively small sample size limits the generalisability of our results and wider sampling should be considered in the future.

Land use effects on egg size

We observed considerable inter-colony variation in egg sizes, consistent with prior findings that genetic factors partially control egg size (Amiri et al. 2020a; Han et al. 2022; Roberts and Taber 1965). Our finding that colonies with recent weight gains yielded smaller eggs, while those with weight losses produced larger eggs aligns with prior

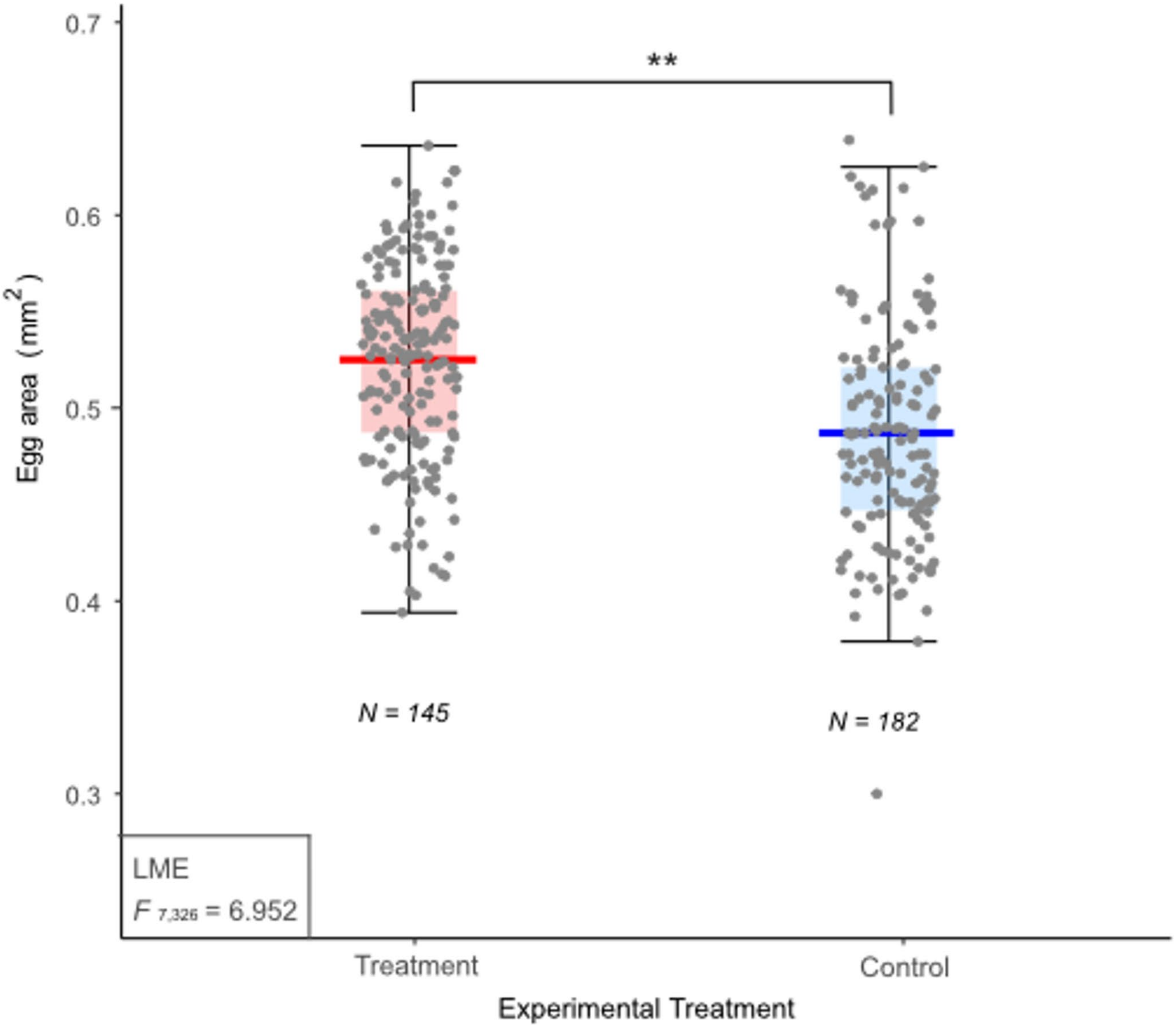

Fig. 6 Egg size differences induced by colony splitting. Plots show the median (thick line), the 25% and 75% quartile ranges (shaded boxes) and individual data points (grey dots). Error bars correspond to data that is up to 1.5 * IQR (Inter Quartile Range) (Table S3 in Online Resource 1)

research showing that in pollen and honey restricted hives queens produce larger eggs (Amiri et al. 2020a). Future studies should include more sites and types of habitats to strengthen our conclusions and better understand land use effects. Although no clear relationships were found in this study (potentially due to a small number of sites) we may expect to see hive weight changes correlated with suburban land proportions, given that suburban areas in southwest England provide ample forage for urban hives during the study period (Tew et al. 2022).

Finding smaller eggs in urban areas may be explained by residential areas offering abundant food sources in gardens and allotments, which can be vital pollinator hotspots (Baldock et al. 2019). Urban forage is also more diverse than rural food sources, including a high percentage of non-native plant species to provide consistent polyfloral pollen and nectar which support bee nutrition (Tew et al. 2021, 2022; Timberlake et al. 2024b). Producing larger eggs as a response to nutritional stress has been observed in other insects, such as *Drosophila melanogaster* and marine invertebrates (Vijendravarma et al. 2010; Marshall and Bolton 2007).

However, other confounding factors may also impact colony nutrition and, therefore, egg size, including different pesticide exposure, pollutants and microclimatic variations. Research suggests 85–90% of total UK pesticide consumption is used in agricultural land and the remainder in urban gardens and allotments, which has deleterious effects for bee

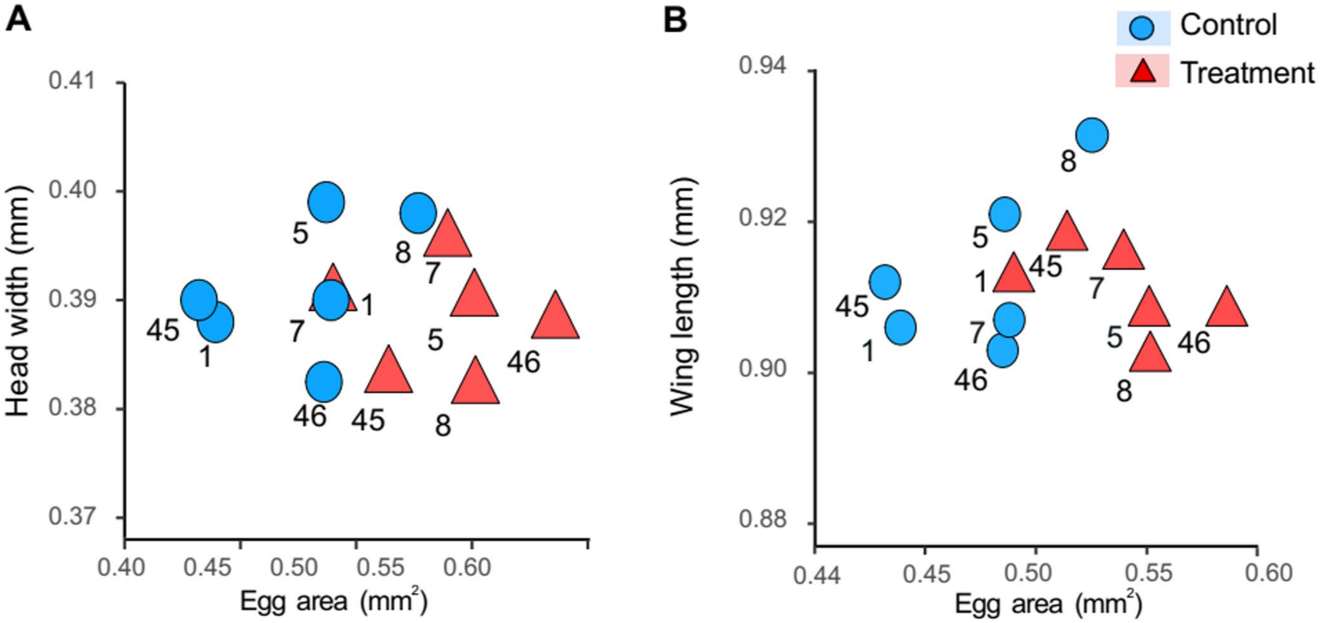

Fig. 7 Honey bee egg size as a predictor of (**A**) worker head width and (**B**) wing length. Eggs from treatment colonies were larger than control colonies. Data split by colony identity (labelled as numbers) (for average colony egg sizes, see Table S3 in Online Resource 1)

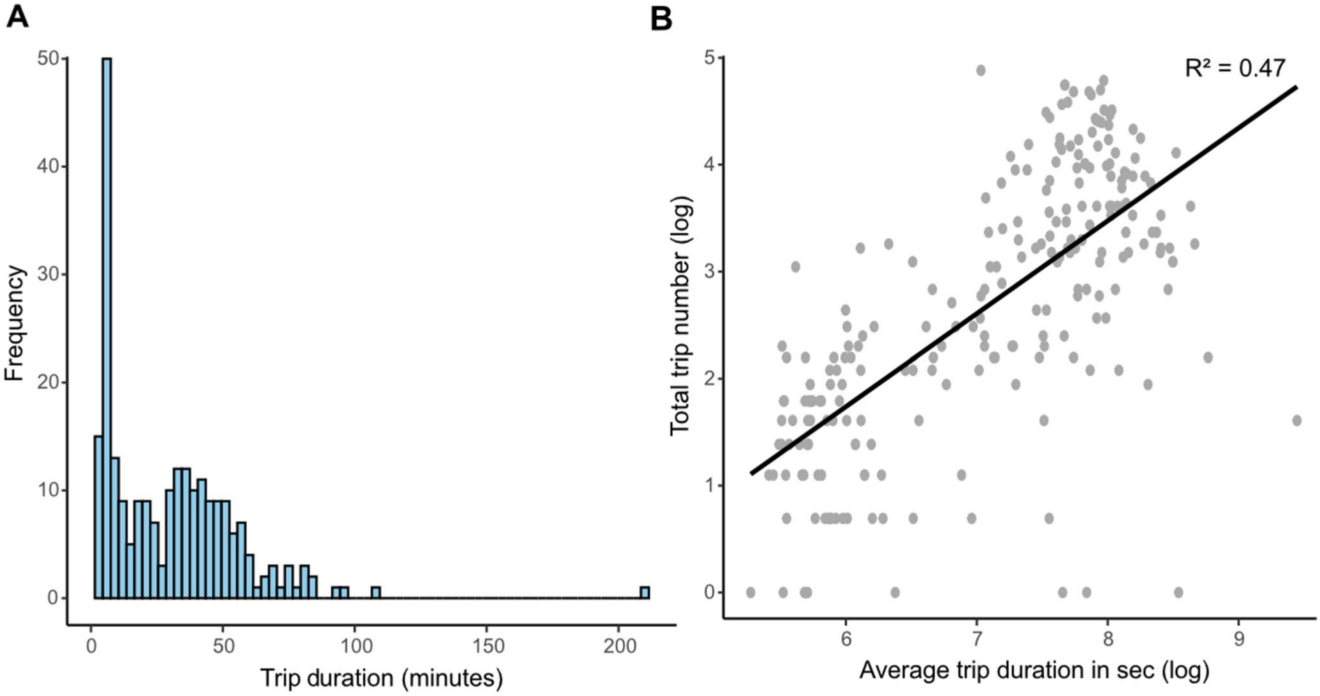

Fig. 8 **A** Average trip duration (*N*=6,346) to show the most frequent average trip time was between 4–9 min. **B** Relationship between number of foraging trips and average trip duration per bee to show a positive relationship between trip number and trip length (*N*=235 bees)

health, reproductive success and foraging decisions (Siviter et al. 2018, 2021a, b; UK Gov 2025). Ryalls et al. (2022) report anthropogenic air pollutants reduce insect pollination by altering floral odours. Urban heat effect causes reduced thermal variability for bee hives in cities, which may impact bees health both negatively by increasing the risk of hive desiccation, and positively by creating temperatures that limit pathogen proliferation (Martín-Hernández et al. 2009; Dalmon et al. 2019; Palmer-Young et al. 2019). Kierat et al., 2017 found that increased temperatures reduced the size of vision cells (ommatidia) which acts as a proxy for cell size in insects and can impair vision with consequences

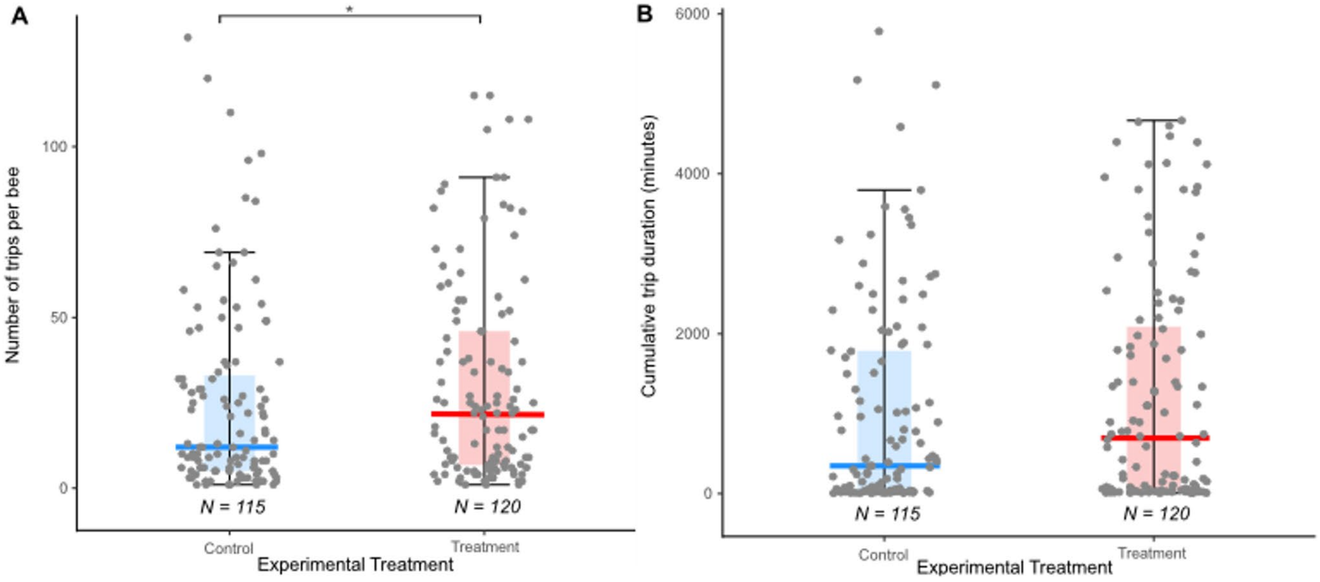

Fig. 9 Treatment effects on foraging activity. **A** Total number of trips (N=6,346) per bee (N=235) as split by treatment with significant difference between treatment groups. **B** Cumulative foraging trip durations per bee with no significant difference between treatment groups

on foraging efficiency, since larger ommatidia support are associated with increased flower detection rates and allow for foraging in dimmer environments (Spaethe and Chittka 2003; Streinzer et al. 2016).

Colony splitting effects on egg and bee size

Experimentally split colonies (with populations reduced by ~70–90%) produced eggs which were on average ~8% larger than eggs from control colonies (Fig. 6). This supports previous findings that queens in smaller colonies lay larger eggs (Amiri et al. 2020a; Han et al. 2022). Further research is needed to determine how queens gauge colony size and how rapidly they can adjust egg size in response to sudden changes in colony conditions. In our study, the adjustment in egg size occurred within three days of splitting the colony, but queens may be able to sense changes in conditions much faster.

The relationship between egg size and bee size is complex (Berrigan 1991; Church, 2019; Fox and Czesak 2000; García-Borros, 2000) as body size is affected by multiple factors, including genetics, nutrition, environmental and social factors (Chole et al. 2019) as has been well documented in honey bees (Amiri et al. 2020a; Wu et al. 2025) or in bumble bees (Fitzgerald et al. 2022; Shpigler et al. 2013). Our analysis revealed a positive, but weak correlation between egg size and bee size. We found a significant interaction between treatment and egg size in their effect on head width (Fig. S3 in Online Resource 2). In control colonies, there was a positive trend suggesting that larger egg sizes were associated with larger head widths. Conversely in treatment colonies, we observed no relationship between egg size and head width. The lack of a clear relationship may be attributed to the overall consistent body sizes in honey bees or potentially the absence of a true effect of colony splitting on head width, most likely because the energy needed to make a bee arises not from the nutrition in the egg but from worker jelly fed by nurse bees. Although our data indicate that both the treatment and egg size had an effect on wing length, the impact of egg size was borderline non-significant. Contrary to our expectation, wing lengths were comparatively shorter in treatment bees compared to control bees (See Fig. S3B in Online Resource 2).

The absence of an obvious relationship between egg size and bee size in our data is supported by Han et al., (2023) who showed that cross fostering bees of small eggs into larger colonies can trigger compensatory growth, which negates the effects of a smaller egg on final body size. This likely happened in our study since we transplanted eggs of different sizes into a large common garden colony which was well provisioned. However, bees produced from large eggs appear to retain some growth advantages when reared in smaller colonies, showing larger body sizes in adulthood than bees reared from smaller eggs (Han et al., 2023).

Considering the behavioural consequences of body size changes, smaller foragers have been recorded in the stingless bee *Melipona quadrifasciata* as a stress response in weak colonies, possibly to allow colony recovery if each forager is able to carry larger amounts of pollen relative to their body weight (Ramalho et al. 1998). Worker size also affects age-dependent behaviour, with larger bees performing age-related tasks earlier than smaller bees (Kerr and

Hebling 1964; Yerushalmi et al. 2006; Hammel et al. 2016). While we did not find a strong link between egg size and worker size, body size plasticity in response to reduced forage deserves further research due its role for foraging ranges (Greenleaf et al. 2007; Grüter and Hayes 2022) and resource carrying capacity (Ramalho et al. 1998; Spaethe and Weidenmüller 2002).

Treatment and egg size effects on foraging performance

Overall, lifetime foraging effort was highly variable, with 17% of worker bees performing 50% of all foraging trips, which is consistent with previous studies (Klein et al. 2019; Tenczar et al. 2014). We found that bees from treatment eggs made ~ 24% more foraging trips, potentially compensating for reduced worker numbers after colony size reduction. Average foraging trip duration increased by only ~ 4% in treatment bees compared with control bees, suggesting treatment increased trip frequency but not trip length. Using egg size as predictor, we again found a positive effect of egg size on foraging trip number, but no effect was found on cumulative foraging trip duration or average foraging trip duration (Table S4). Neither egg size nor treatment had a significant effect on age of first or last foraging or on foraging lifespan (Table S4).

While Amiri et al. (2020a) found that larger eggs increase brood survival rates, we found no effect of egg size on adult bee lifespan. Therefore, we might consider how larger eggs produce bees with altered behavioural phenotypes without an influence on morphology or lifespan. If larger eggs contained elevated hormones or nutritional factors that primarily increase motivation to forage, we would expect a decrease in lifespan because foraging is a risky behaviour (Visscher & Dukas 1997). Alternatively, larger eggs may produce bees that are better foragers or more resilient to metabolic stress. Studies examining the contents of honey bee eggs report that larger eggs show a higher relative number of metabolites, with more mass and better nutrients for the developing larvae (Han et al., 2023) potentially triggered by the upregulation of queen ovarian proteins related to energy metabolism, growth and cytoskeleton development (Han et al. 2022).

Additionally, it is unknown if there is a trade-off for queens between egg size and number laid (see Amiri et al. 2020a; Han et al. 2022 for contrasting findings). Since the burden of foraging is shared among colony members, the trade-off may be weaker in social bees than in solitary organisms (Amiri et al. 2020a; Han et al. 2022). Future experiments could correlate egg size with queen egg-laying rate and maternal longevity.

Nurse bee food provisioning significantly influences offspring development, and in the mass-provisioning stingless bees and in bumblebees, the final size of the worker is determined by the amount of food provisioned by the nurses before oviposition and the sealing of the cell (Couvillon and Dornhaus 2009; Segers et al. 2015). In honey bees, relative amounts of protein and carbohydrates have been shown to affect worker size, with bees on high protein diets being lighter and smaller, whilst those on high carbohydrate diets display more variation in body mass (Nicholls et al. 2021). Egg size may not directly correlate with worker size and behaviour if nurse bees can assess egg size and adjust feeding accordingly (Han et al., 2023).

Conclusions and outlook

This study demonstrates that egg size may be linked to nutritional conditions in rural and urban habitats, and increased egg size was associated with increased foraging. Our findings suggest that anthropogenic land use change may drive life-history adjustments within honey bee colonies, with urban gardens providing critical forage that influences hive stores and reduced egg sizes. While manipulation of egg size led to increased foraging trips by workers, it did not affect their lifespan, implying that queens may be able to enhance overall colony foraging activity without altering individual worker longevity.

The mechanisms underlying the relationship between egg size and foraging activity remain unresolved. Although there is evidence that larger eggs provide more resources to developing workers (Han et al., 2023), exactly how this increases foraging activity or "motivation to forage" in workers is unknown. Future research should aim to resolve how bee eggs of different sizes and their constituents affect worker physiology and behaviours such as aggression, nursing or hygiene/cleaning, and whether there are any associated survival costs (Amiri et al., 2020a).

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Author contributions K.G. and C.G. designed the study. R.K. and Y.W. helped with data collection, colony set up and colony maintenance. K.G. and C.G.and conducted the field work and analyzed the data, K.G. wrote the first draft, and all authors reviewed and approved the final manuscript.

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Data availability Raw foraging data can be accessed from repository (DOI [https://doi.org/10.5061/dryad.sxksn03g9](https:/doi.org/10.5061/dryad.sxksn03g9)).

Declarations

Competing interests The authors declare no competing interests.

Statement of significance Land use change affects bee populations by changing their food supply and nutritional health. We found that rural land use types are associated with larger eggs. To understand the significance of this egg-size plasticity, we measured worker size and foraging efforts from bees of both large and smaller eggs. Bees from larger eggs were similar in body size, but they performed ~ 24% more foraging trips. The duration of each foraging trip was not affected by egg size. Neither body size nor lifespan were associated with egg size, and the mechanism causing increased foraging remains unknown. Further studies are needed to clarify how egg size may fit into a broader suite of colony-level responses to environmental change and nutritional stress.

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