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SHORT COMMUNICATION

Distance estimation by Asian honey bees in two visually different landscapes

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ABSTRACT

Honey bees estimate distances to food sources using image motion experienced on the flight path and they use this measure to tune the waggle phase duration in their dance communication. Most studies on the dance-related odometer are based on experiments with *Apis mellifera* foragers trained in small tunnels with black and white patterns, which allows the creation of quantifiable changes in optic flow. In this study, we determined the waggle phase duration–distance curves of two Asian honey bee species, *Apis florea* and *Apis cerana*, in two different natural environments with clear differences in the vegetation conditions and hence visual contrast. We found that the dense vegetation condition (with higher contrast) elicited a more rapid increase in the waggle phase duration with distance than the sparse vegetation condition in *A. florea* but not in *A. cerana*. Our findings suggest that contrast sensitivity of the waggle dance odometer might vary among honey bee species.

KEY WORDS: *Apis cerana*, *Apis florea*, Optic flow, Visual contrast, Waggle dance

INTRODUCTION

Honey bees, like other flying insects, mainly use image motion (optic flow) in their environment to estimate flight distances (Esch and Burns, 1996; Lecoeur et al., 2019; Srinivasan et al., 1996; Srinivasan, 2011). Studies in *Apis mellifera* established that it is this optic flow-driven odometer, and not time of flight or energy consumption, which is used to tune the waggle phase duration, the distance signal of the dance communication (Dacke and Srinivasan, 2008; Esch et al., 2001; Srinivasan et al., 2000). The odometer is based on contrast information in the green spectral channel and even very low levels of contrast are sufficient for the honey bee's visual system to detect and process image motion information (Chittka and Tautz, 2003; Si et al., 2003). Most of these findings are based on studies in which foragers were trained in a small tunnel, which allowed a controlled manipulation of the visual environment (Esch et al., 2001; Srinivasan et al., 2000).

Studies on how the waggle phase duration varies in natural habitats, with apparent differences in optic flow information, are rare (Esch and Burns, 1996; Esch et al., 2001; Tautz et al., 2004). Tautz et al. (2004) compared waggle phase durations for feeder locations on land and

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water. In line with their expectation, the slope for the relationship between waggle phase duration and feeder distance ('calibration curve') was higher on land than on water. However, water is an extreme environment with respect to honey bee foraging, and the authors also reported that no recruits visited the feeder when it was over water. Thus, our knowledge of whether and to what extent odometric calibration curves of honey bee colonies vary between natural environments which differ in their vegetation density is scarce (Collett, 2000). Apart from variation in contrast, the flight height of foragers may also differ depending on the environment, which in turn affects the perceived optic flow and waggle dance information (Baird et al., 2021; Esch and Burns, 1996). In this study, we present a comparison of calibration curves of the same colonies between a dense and a sparse vegetation environment for two different Asian honey bee species, *Apis florea* and *Apis cerana*.

Apis florea, the open-nesting red dwarf honey bee species, is phylogenetically distant from cavity-nesting species such as *A. cerana* and *A. mellifera* (Raffiudin and Crozier, 2007; Smith, 2020). *Apis florea* differs markedly from the two very similar cavity-nesting species in size, nesting environment and the variety of signals produced in the waggle dance (Dyer, 2002; I'Anson Price and Grüter, 2015). The waggle dance in *A. florea* occurs on the horizontal surface at the top of the comb and is directed towards the food source (Dyer, 1985). In the cavity-nesting *A. cerana*, foragers perform dances on vertical combs (Lindauer, 1956; von Frisch, 1967). In spite of these differences, the two species show strong similarities in the relationship between the waggle phase duration and foraging range, the change in dance precision with distance and the dance follower behaviour (Beekman et al., 2015; George et al., 2020; Kohl et al., 2020; Sen Sarma et al., 2004). *Apis florea* and tropical *A. cerana* have similarly 'steep' calibration curves which increase with distance more rapidly than those of the temperate *A. mellifera* (Kohl et al., 2020). Given that *A. florea* and *A. cerana* have similar calibration curves while being phylogenetically very distant in this genus, they are well suited to explore possible species differences in the dance odometer.

We studied the effect of two different natural environments, with different vegetation conditions and hence visual contrast, on three aspects of the waggle dance behaviour: the waggle phase duration, the return phase duration and the number of dance circuits performed per dance in *A. florea* and *A. cerana*. Crucially, we tested foragers from the same colony in both the dense and sparse vegetation condition by shifting the whole colony from one condition to the other. We were interested in exploring whether natural variation in optic flow information differently affects the waggle dance behaviour in these Asian *Apis* species.

MATERIALS AND METHODS
Colony preparation and experimental location
The experiments were performed with a wild *Apis florea* Fabricius 1787 colony located on the National Centre for Biological Sciences,

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Bangalore campus and an *Apis cerana* Fabricius 1793 colony bought from a commercial beekeeper. In both species, the colony was first shifted to the dense vegetation environment with high visual contrast – the Botanical Garden of the University of Agricultural Sciences, Gandhi Krishi Vignana Kendra, Bengaluru, India (Fig. 1A). After experiments in the Botanical Garden, the colony was shifted to an open field in the same campus with sparse vegetation and hence low visual contrast (Fig. 1B). In the case of *A. florea*, the colony was placed in a box that allowed video recordings of the crown area of the colony where the foragers perform the waggle dance (Dyer, 1985). In the case of *A. cerana*, the colony was kept in an observation hive with the individual frames placed horizontally next to each other. The wall of the hive closest to the entrance was made of glass, which allowed recordings of the dance floor area. The experiments in the botanical garden have been described previously (Kohl et al., 2020), although the dance analysis for the current paper was done separately.

Experimental protocol

The same experimental protocol was followed for both species in the two environments. The colony was shifted into the location in the evening, to ensure that most foragers had returned to the colony before the shift. The colony was allowed to rest for a day and then training was initiated the next morning. Foragers from the colony were trained based on established protocols to an artificial feeder filled with sucrose solution placed next to the colony (Scheiner et al., 2013). The sucrose concentration of the feeder ranged from 1 to 1.5 mol l^{-1}, depending on the number of foragers visiting the food source. Once 10–20 foragers were coming to the feeder on

their own, the feeder was shifted in steps of 5–10 m to 25 m. At 25 m, the foragers were individually marked (Uni POSCA Paint Markers, Uni Mitsubishi Pencil).

The feeder was then shifted in small steps to 100 m and the foragers active at the feeder were observed in the hive. Their dance activity was recorded using a Sony HDR-CX240 at 50 frames s^{-1}. After recording for an hour at this distance, we shifted the feeder to the next distance of 200 m for the next set of video recordings. This protocol was repeated for distances of 300, 400 and 500 m over a period of 5 days, following which the colony was shifted to the open field. We had to train foragers again in the open field and so could not ensure that the same individual foragers were active at our feeder in the two conditions. Both the experimental locations represent habitats generally used by the two species in Bangalore and foragers from other colonies were observed foraging at both sites.

Contrast analysis

To quantify the difference in the visual contrast between the dense and the sparse vegetation conditions, we analysed the amount of contrast in images from the two conditions following the protocol in Tautz et al. (2004). We obtained 5 images each, at a resolution of 4928×3264 pixels, from the two conditions. The images were obtained at distances of 100, 200, 300, 400 and 500 m facing away from the hive and towards the feeder (Fig. 1; Fig. S1). The average of the intensity of the red, green and blue channels for each pixel was obtained from the images. The contrast was then calculated as the standard deviation of the average pixel intensity divided by the mean of the average pixel intensity. We calculated the contrast for four different sections of the image: the full image, a horizontal
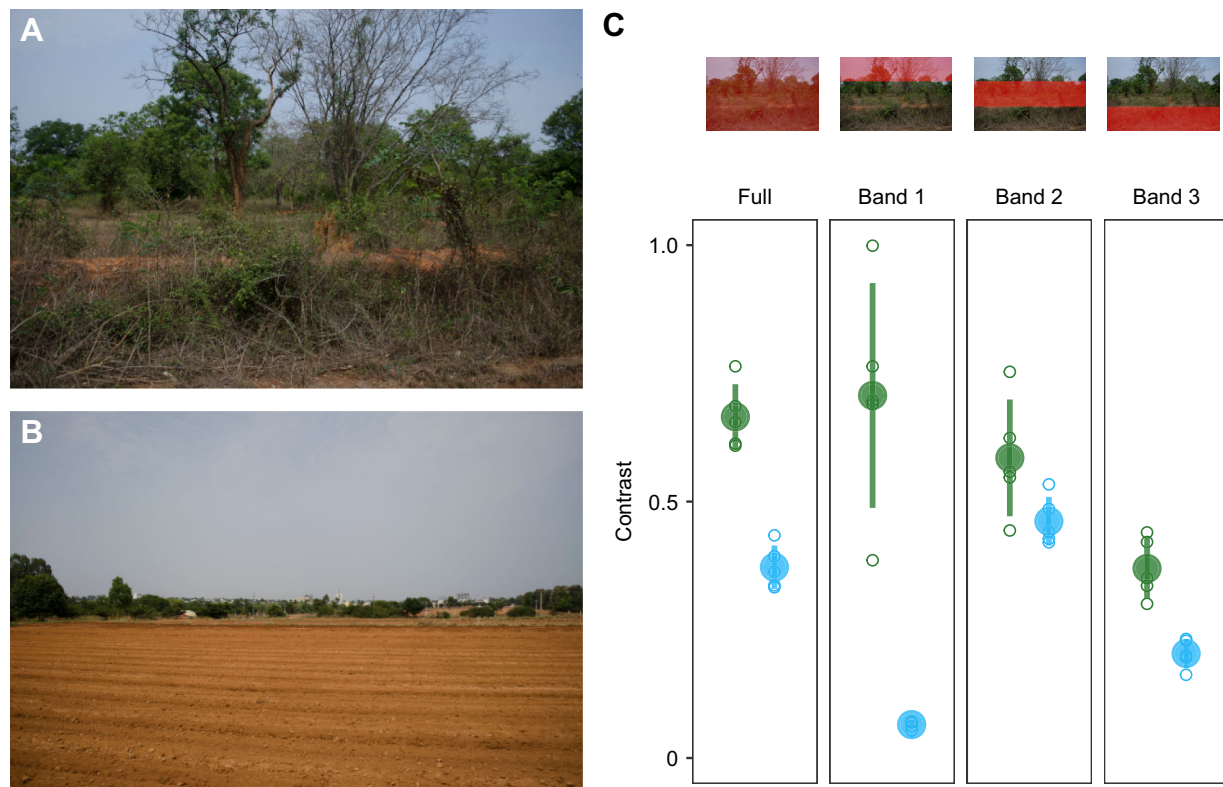
Fig. 1. The study sites. Representative images of (A) the dense and (B) the sparse vegetation conditions, taken at 200 m in the direction away from the hive location, towards the feeder location. (C) The amount of contrast present in the five images from each condition. The filled circles and error bars correspond to the mean and standard deviation of the two conditions and the open circles correspond to the contrast obtained from the individual images (green, dense vegetation; blue, sparse vegetation).

band covering the top third of the image (band 1), a horizontal band covering the middle third of the image (band 2) and a horizontal band covering the bottom third of the image (band 3). We then compared the level of contrast in each of these sections between the two vegetation conditions. We compared the contrast in the whole images as well as contrast in the different bands to check whether the overall difference in contrast was reflected in arbitrary smaller sections of the image.

We used a linear model with the contrast value as the response and the vegetation condition as the predictor and found that there was a strong difference in the contrast between images from the dense and sparse vegetation conditions (Fig. 1C, difference estimate between dense and sparse=0.293, t=8.59, P<0.0001). To compare the contrast levels within the three horizontal bands, we first built two linear models: one with the contrast as the response, and the condition and the band identity as the predictors, and another with the same response and predictors, but with an interaction term between the predictors. On comparing these two models, we found that the model with the interaction was significantly better at explaining the data (F=18.375, P<0.0001). We then checked the model with interactions and found that the dense vegetation condition had significantly higher contrast than the sparse vegetation condition in band 1 and band 3 (Fig. 1C, band 1: difference estimate between dense and sparse=0.642, t=9.56, P<0.0001; band 2: difference=0.124, t=1.84, P=0.078; band 3: difference=0.166, t=2.47, P=0.021).

Video analysis
We followed established protocols for analysing the waggle dance activity (Seeley, 1995). The honey bee waggle dance consists of a waggle phase, which is very short at distances close to the hive, and a return phase (Gardner et al., 2008). The first frame in which a bee moved its abdomen dorsoventrally or laterally while starting a forward motion was considered as the start of the waggle phase and the frame in which the bee stopped moving its abdomen before turning away from a straight path was considered as the end of the waggle phase. The return phase was the time period between the end of one waggle phase and the start of the next. The number of dance circuits was equivalent to the number of waggle phases in the dance. In *A. florea*, we analysed a total of 34 dances in the dense condition (dances per distance: 6.8±2.39 mean±s.d.) and 36 dances in the sparse condition (7.2±1.79) while in *A. cerana*, we analysed a total of 50 dances each (10 dances per distance) for the two conditions (Table S1).

Statistical analysis
We analysed the effect of visual contrast on the waggle phase duration, the return phase duration and the number of dance circuits in both species separately. We used mixed effects models to determine the effect of distance and vegetation (visual contrast) condition on each of the parameters while accounting for differences amongst bees in the slope of the relationship between the parameter of interest and distance. The models had the respective parameter as the response variable, an interaction between the distance (a continuous variable) and the visual contrast condition (a categorical variable of two levels) as the predictor, and bee ID as a random effect on the slope.

In the case of the waggle phase duration and the return phase duration, the analysis was done on the mean duration of all the phases in each dance, and not on the individual phases themselves. We first fitted linear mixed-effects models (LMMs) for the two response parameters. However, in most cases, model assumptions were not validated because of the non-linear distribution of the data

(Figs 2A and 3A) and, as a result, we did not make inferences from the LMMs. Instead, we fitted non-linear mixed-effects models (NLMMs) with the logarithmic regression as the non-linear function. The logarithmic regression was of the form:

$$Y = a + b \times \log(X). \tag{1}$$

The NLMMs were used to estimate and compare the values of a and b for the two vegetation conditions. As a and b are analogous to the intercept and slope in a linear regression, for simplicity's sake we refer to them as the intercept and slope henceforth. We were primarily interested in quantifying the effect of the visual contrast on the slope b. To understand the value of the slope, consider the equation for the logarithmic regression given above. For a change in distance by 1% from 100 m to 101 m, the change in waggle phase duration is:

$$(a + b \times \log 101) - (a + b \times \log 100), \tag{2}$$
$$(b \times \log 101) - (b \times \log 100), \tag{3}$$
$$b \times (\log 101 - \log 100), \tag{4}$$
$$b \times \log\left(\frac{101}{100}\right). \tag{5}$$

$\log(101/100)$ is equal to 0.00995 or approximately 0.01. Thus, a 1% change in distance corresponds to a change in waggle phase duration equivalent to b×0.01 or b/100. Similarly, a 10% change in distance would correspond to a change in waggle phase duration approximately equal to b/10 (as log1.1 is equivalent to 0.095 or approximately 0.1). While Y and X are measured in seconds (s) and metres (m), respectively, the unit of the slope is not s/m because of the logarithmic transformation on X. We verified the model assumptions of homoscedasticity and normality of the residuals for NLMMs, and they were validated in all cases except one. The NLMM for waggle phase duration in *A. cerana* showed signs of heteroscedasticity. To account for this, we provided a power variance function structure with a function coefficient of 10 (determined by trial and error) on the variance covariate 'distance'. In the case of the number of dance circuits, we fitted a negative binomial mixed-effects model to account for the discreteness as well as the overdispersion in the data (Table S2).

All the statistical analysis was performed in R 4.0.1 (http://www.R-project.org/), using the RStudio IDE (http://www.rstudio.com). We used the aomisc (https://github.com/OnofriAndreaPG/aomisc) and nlme package (https://CRAN.R-project.org/package=nlme) to fit the LMMs and the NLMMs, and the glmmTMB package (Brooks et al., 2017) to fit the negative binomial mixed-effects models. We used the ggplot2 (Wickham, 2016), gghalves (https://github.com/erocoar/gghalves) and cowplot (https://wilkelab.org/cowplot/) packages to visualise the model fit and the data. Additionally, we used pillow (https://pypi.org/project/Pillow/), numpy (Oliphant, 2006) and pandas (McKinney, 2010) packages in python (https://www.python.org/) to extract the contrast values from photographs. A primer on how to fit NLMMs, the R code we used, as well as details of additional analyses exploring the non-linearity in the waggle phase duration are available from Zenodo (https://zenodo.org/record/4561224).

RESULTS AND DISCUSSION
The principal finding of our study is that *A. florea* and *A. cerana* foragers responded differently to the two visual environments as indicated by the waggle phase duration–distance calibration curves. All calibration curves showed an increase with feeder distance
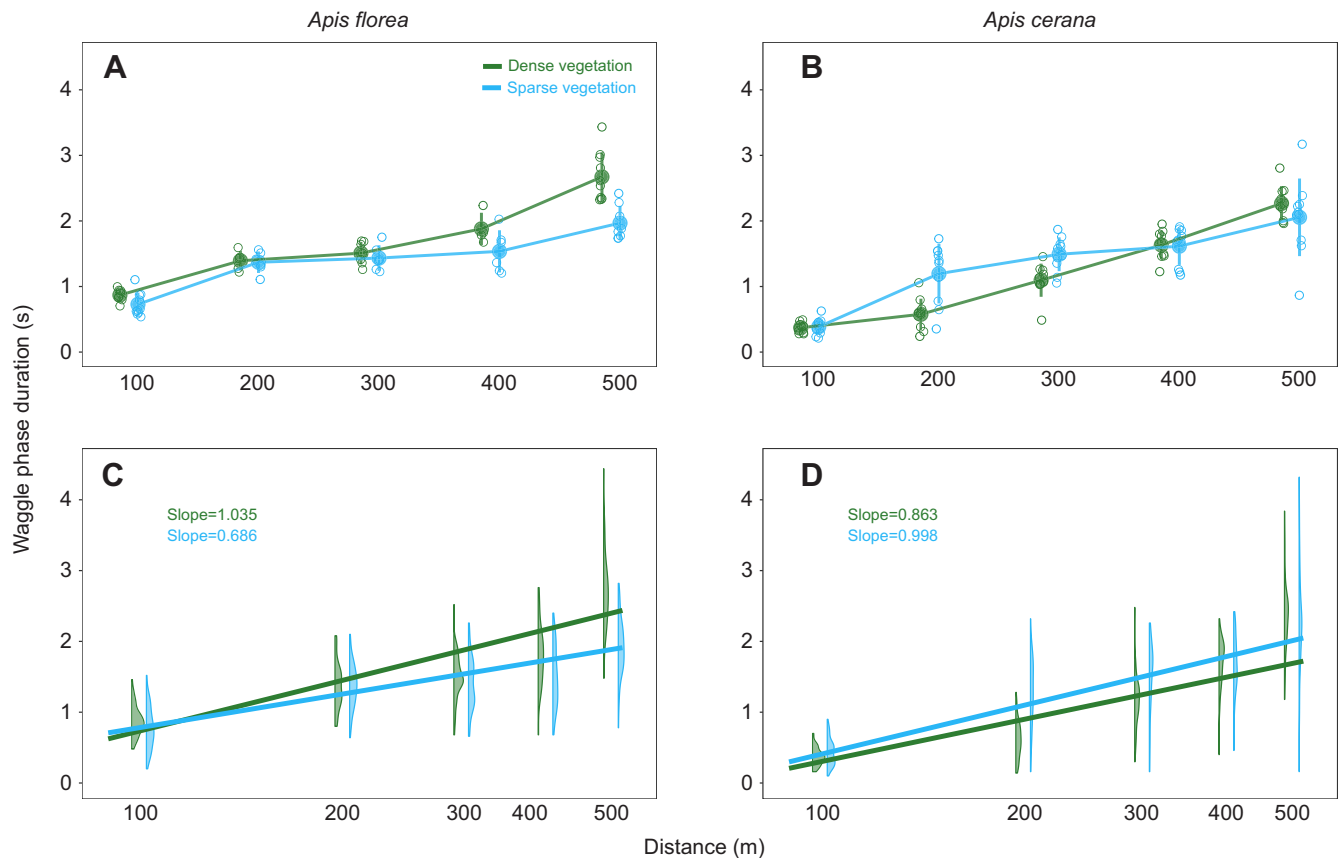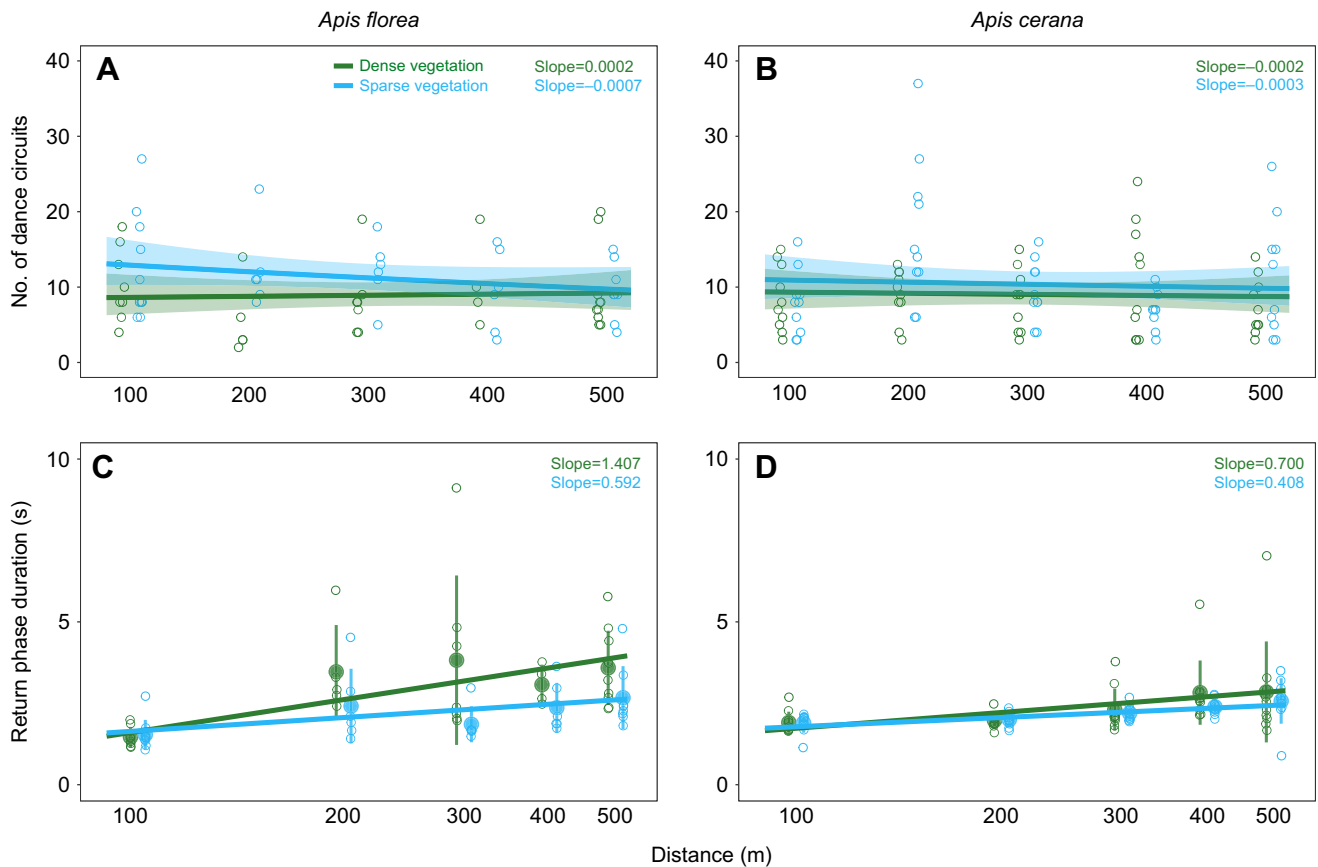
Fig. 2. The waggle phase duration at different distances in the two vegetation conditions for *Apis florea* and *Apis cerana*. (A,B) The mean waggle phase duration for individual dances (open circles), along with the mean for all the dances and the standard deviation (filled circles with error bars) for *A. florea* and *A. cerana*, respectively. (C,D) The predicted fits obtained from the non-linear mixed-effects logarithmic regression model (lines) and the distribution of individual runs at each distance (shown on a log scale) for *A. florea* and *A. cerana*, respectively. The slope values, circles, fitted lines and distributions are coloured based on the vegetation condition (green, dense vegetation; blue, sparse vegetation).

independent of the environment. However, only in *A. florea* was the slope of the calibration curve in the visually more cluttered environment significantly higher (by 1.5-fold) compared with that in the open field (Fig. 2A,C; difference estimate between slopes in dense and sparse condition=0.349, confidence interval=0.116–0.581, t=2.921, P=0.005). In *A. cerana*, the calibration curves for the two environments did not differ significantly (Fig. 2B,D; difference estimate=−0.135, confidence interval=−0.332–0.062, t=−1.336, P=0.186). These results suggest that the estimation of flight distance and subsequent dance information in natural environments might be more complex than predicted by flight responses in spatially restricted tunnels with controlled black and white patterns.

Tunnel experiments showed that the dance odometer in *A. mellifera* is driven by contrast in the green spectral channel (Chittka and Tautz, 2003) and that a large change in contrast between vertical stripes (from 20% to 92%) leads to a 1.5-fold change in the waggle phase duration for the same tunnel distance (Si et al., 2003). Unfortunately, there is only one study so far that has tried to estimate the effect of optic flow on the waggle dance in two visually distinct environments, over land and over water (Tautz et al., 2004). A change in contrast from around 9% (over water) to around 20% (over land) led to a 4-fold increase in the slope of the calibration curve. So, both types of experiments clearly indicate that contrast affects distance estimation and waggle phase duration. However, the relationship between contrast differences in the

landscape and perceived optic flow is unclear. For example, Si et al. (2003) suggested that their results favoured a threshold model and concluded that the odometer is robust against a large range of contrast variation, beyond a minimum contrast level. But, there were significant changes in the waggle phase duration beyond this threshold in their experiments. It should be noted that the contrast differences in the field and tunnel experiments were calculated in different ways. In the field experiments, the contrast was calculated from sections of images that recaptured the assumed visual scene experienced by the bee, whereas the contrast calculation in the tunnel experiments was based on the whole flight path experienced by the bee. Obviously, more experiments are needed to clarify the effect of contrast variation on the flight and dance odometer.

Nonetheless, based on previous studies, we expected to observe significant differences in the slopes between the dense and sparse vegetation in both species. Thus, the question arises why did we not find these differences in *A. cerana* but did so in *A. florea*? Foragers from both species were found naturally foraging in and around both visual environments (E.A.G., N.T. and P.L.K., personal observations), and both species nest and forage in diverse types of landscapes (Bakker, 1999; Free, 1981). The observed species differences might be explained by physiological and behavioural differences rather than differences associated with living in different ecological habitats. As contrast has an effect on the flight odometer, differences in contrast sensitivity among honey bee species could affect the calculation of flight distance and waggle phase duration.

Fig. 3. The number of dance circuits and the return phase duration at different distances in the two vegetation conditions for *A. florea* and *A. cerana*. (A,B) The number of dance circuits in each dance (open circles) along with the predicted fits and confidence interval at the fixed effects level (lines and shaded region) from the negative binomial mixed-effects model. (C,D) The mean return phase duration for individual dances (open circles), the mean for all the dances and the standard deviation (filled circles with error bars) at each distance (shown on a log scale), and the predicted fits obtained from the non-linear mixed effects logarithmic regression model (lines). In all four plots, the slope values, circles, lines and shaded region are coloured based on the vegetation condition (green, dense vegetation; blue, sparse vegetation).

Interestingly, a recent tunnel experiment with *A. cerana* and *A. mellifera* foragers reported clear differences in the flight responses to artificial black and white patterns between the foragers of both species (Chakravarthi et al., 2018). The authors of that study concluded that the behavioural differences suggest strong differences in the spatial resolution and contrast sensitivity of the visual system, which were not expected based on the morphological similarities of the eyes of *A. mellifera* and *A. cerana* (Kelber and Somanathan, 2019; Streinzer et al., 2013). Furthermore, honey bee species might differ in their flight behaviour, which in turn affects the odometer (Collett et al., 2006; Esch and Burns, 1996). Foragers regulate their distance from the ground during flight to maintain a constant rate of optic flow (Baird et al., 2021; 2006; Portelli et al., 2010). Species-specific preferences for flight height may thus affect the perceived change in optic flow in different environments, offering an alternative explanation for the differences we see between *A. florea* and *A. cerana*.

In contrast to the results regarding the flight and dance odometer, the parts of the dance that are related to the perceived food reward, i.e. the number of dance circuits and duration of the return phase, showed the expected correlation (Barron et al., 2007; George and Brockmann, 2019; Hrncir et al., 2011; Łopuch and Tofilski, 2020; Seeley, 1989; 1986; Seeley et al., 2000; Shafir and Barron, 2010; von Frisch, 1967). In both species, the number of dance circuits was not affected by distance or the vegetation condition (*A. florea*, difference

estimate=0.0009 circuits m^{-1}, confidence interval=−0.0006–0.0023, z=1.165, P=0.244, Fig. 3A; *A. cerana*, difference estimate=0.0001 circuits m^{-1}, confidence interval=−0.0014–0.0015, z=−0.134, P=0.893, Fig. 3B), whereas the return phase duration slightly increased with distance but was not affected by vegetation condition (*A. florea*, difference estimate=0.815, confidence interval=−1.102–0.732, t=1.730, P=0.089, Fig. 3C; *A. cerana*, difference estimate=0.292, confidence interval=−0.204–0.787, t=1.148, P=0.255, Fig. 3D). Similar to previous distance training experiments in honey bees, we used high sugar concentrations to keep the foragers motivated to dance and recruit throughout the experiment (Seeley, 1995; von Frisch, 1967). This probably led to a ceiling effect which prevented a decline in the number of dance circuits with distance (Seeley, 1994). Regarding the return phase duration, Seeley et al. (2000) demonstrated an effect of the reward value on the return phase by increasing the sugar concentration of a feeder at one distance: the higher the sugar concentration, the faster the return phase. This response makes the dance appear more intense or 'lively' as Lindauer (1948) called it (see also Boch, 1956). An increase in the distance of a food source with the same energetic value should lead to a lowered perception of the reward value (because of the higher energy costs associated with flight) and an accompanying increase in the return phase duration, consistent with our results. Alternatively, the increase in return phase duration could also be linked to the increase in waggle phase duration with

distance, which necessitates a longer return phase to get back to the starting point of the waggle phase and complete the waggle circuit (Heran, 1956). Interestingly, the results for the return phase duration differ from observations on *A. mellifera* by Tautz et al., (2004), who reported that the slope of the return phase duration with distance over water (i.e. low visual contrast) was higher than that over land. However, the authors of that study note that they did not find any recruits at the feeder when the food source was over water (Tautz et al., 2004). The presence of the food source at an unnatural location (over water) for honey bee foragers could explain the unexpected results they obtained regarding the return phase duration.

To conclude, our results indicate that there might be differences in the effect of visual contrast conditions on the odometer amongst honey bee species. However, this species-specific odometer might be more robust against ecologically realistic variation of the visual terrain than a comparison of dance durations over water and land in *A. mellifera* had suggested. This robustness would ensure that honey bee foragers are able to effectively communicate the location of food sources even in heterogeneous environments with varying optic flow along their foraging routes. Additionally, honey bee species may also differ in aspects of their flight behaviour, e.g. flight height, that affect the perception of contrast and thus the odometer. More experiments are needed focusing on the relationship between species-specific differences in the visual system and flight behaviours that drive the odometer used for the waggle dance.

Acknowledgements

Competing interests

The authors declare no competing or financial interests.

Author Contributions

Conceptualization: E.A.G., P.L.K., A.B.; Methodology: E.A.G., P.L.K., A.B.; Formal analysis: E.A.G., N.T., S.S.; Investigation: E.A.G., N.T., P.L.K., B.R.; Writing – original draft: E.A.G., A.B.; Writing – review & editing: E.A.G., N.T., P.L.K., S.S., B.R., A.B.; Supervision: A.B.; Funding acquisition: A.B.

Funding

Data availability

Data files associated with this paper are available from Zenodo: https://zenodo.org/record/4561224

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