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Homing ability in a tropical Asian stingless bee is influenced by interaction between release distances and urbanisation

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Abstract

1. Bee homing capacity determines the maximum distance/area from/around the nest that workers can travel to exploit resources. However, homing ranges have been hardly examined in tropical Asian stingless bee species or in relation to anthropogenic land-use changes.
2. Here, we used translocation experiments, where we released marked bees at different distances from the colony, to evaluate the maximum homing distance of *Tetragonula fuscobalteata* in 10 different anthropogenic landscapes in Southern Thailand.
3. Our results show that typical and maximum homing distances (i.e., distances where 50% and 90% of released bees failed to return, respectively) were estimated to be 240 and 595 m, respectively. We found that bee homing rates were not affected by forest proximity or surrounding landscape composition within 100, 200, 300, 400, 500 and 600 m radii, but that they were influenced by the interaction between release distances from the colony and the proportion of urbanised cover at a 100 m radius. Bee homing rates decreased with increasing release distances for colonies placed in areas with higher proportions of urbanised land within a 100 m radius.
4. This suggests that urbanised areas (e.g., urban or suburban gardens, home gardens, backyards) provided sufficient food resources close to colonies, resulting in smaller foraging ranges.

KEYWORDS

anthropogenic landscapes, foraging ranges, homing distances, translocation experiment, urbanised area

INTRODUCTION

Currently, bees, like other insects, are threatened by multiple stressors (e.g., land-use change, climate change, agricultural intensification, introduced species, nitrification, pollution, pesticides and urbanisation [Wagner, 2020; Wagner et al., 2021]), and their diversity has declined worldwide (Zattara & Aizen, 2021). Many of these stressors are known to directly or indirectly affect the availability of resources foraged by bees (Roulston & Goodell, 2011). Importantly, bees (Hymenoptera, Apidae) are central-placed foragers (i.e., nest-dwelling), where foragers need to depart from and return to a specific nesting site (Minahan & Brunet, 2018). Stressors-induced variation in the availability of resources surrounding the nest may consequently affect their foraging ranges, that is, the maximum distance from the nest that individuals travel and forage. Understanding how land-use affects the homing ability and hence foraging ranges of different bee species is important for supporting bee conservation and tailoring land management to maintain pollination services.

Bee foraging ranges can be predicted by their body size (i.e., intertegular [IT] span) following Greenleaf et al. (2007). However, as

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foraging ranges likely also depend on the structure of the surrounding landscape (Leonhardt et al., 2016), estimated foraging distances may be largely different from actual foraging ranges, which can only be revealed through field experiments with specific bee species. There are four common techniques previously applied to estimate foraging distances in bees: (1) for honey bee species (*Apis* spp.), the 'waggle dance' can be decoded to give typical foraging ranges (e.g., Beekman & Ratnieks, 2000), (2) for large bee species, radar tracking can provide exact foraging paths (e.g., *Bombus terrestris* was equipped with a lightweight radar transponder (Osborne et al., 1999), and some stingless bee species (*Melipona* spp.) were equipped with passive radio-frequency identification (RFID) tags (Costa et al., 2021; Nunes-Silva et al., 2020). Moreover, RFID technology can provide information on bee foraging times spent outside the nest (Oliveira et al., 2021). Next, (3) for most species, training to an artificial feeder (which is then moved further and further away from the nest) can be used to reveal maximum foraging distances (e.g., Kaehler et al., 2021; Kuhn-Neto et al., 2009; van Nieuwstadt & Ruano Iraheta, 1996). This technique may prove difficult if natural foraging sources are abundant, and bees are reluctant to feed from an, less conspicuous, artificial feeder or readily abandon it (Smith et al., 2017; van Nieuwstadt & Ruano Iraheta, 1996). Finally, (4) translocation experiments, where bees are caught and released at increasing distances from the colony, can be used to obtain the percentage of bees that return from each distance to estimate the homing/foraging range, that is, the area surrounding the nest where bees can still orientate (e.g., Campbell et al., 2019; Gathmann & Tscharntke, 2002; Leonhardt et al., 2016; Smith et al., 2017; van Nieuwstadt & Ruano Iraheta, 1996).

In subtropical and tropical regions, stingless bees (Apidae: Meliponini) are key pollinators for both wild and agricultural crops (Borges et al., 2020; Hansen et al., 2020; Heard, 1999; Momose et al., 1998; Ramírez et al., 2018; Slaa et al., 2006; Sritongchuay et al., 2021). They are eusocial bees and live in perennial colonies consisting of a single queen and hundreds to thousands of workers (Michener, 2007). Several meliponine species are managed for crop pollination as well as honey and pollen production, which is referred to as meliponiculture (Cortopassi-Laurino et al., 2006; Slaa et al., 2006). However, like many other wild bees, stingless bee communities are impacted and altered by anthropogenic land-use change (Brosi, 2009; Brown & Albrecht, 2001; Lichtenberg et al., 2017; Wayo et al., 2020) likely as a consequence of altered resource landscapes (Requier & Leonhardt, 2020; Roulston & Goodell, 2011). All required resources for stingless bees (i.e., pollen, nectar, water, resins) are patchily distributed throughout landscapes and their availability largely depends on landscape composition. When faced with resource changes, such as a reduced density of resources available in the surrounding landscape, bees will adjust their foraging ranges accordingly. For example, they typically forage at relatively short distances in resource-rich landscapes but expand foraging distances in resource-poor landscapes with a patchy distribution of resources (Ogilvie & Forrest, 2017). This may also explain why homing distances of stingless bees were found to change with season (Campbell et al., 2019) and landscape type, that is, bees tagged with RFID had higher return rates when released in forests than when released in the neighbouring mining area (Costa et al., 2021).

Previous homing studies in stingless bees were mostly undertaken in the Neotropics (e.g., Campbell et al., 2019; Costa et al., 2021; Rodrigues & Ribeiro, 2014; Roubik & Aluja, 1983; Silva et al., 2014; van Nieuwstadt & Ruano Iraheta, 1996) and in Australia (e.g., Leonhardt et al., 2016; Smith et al., 2017). However, homing distances have not yet been investigated in tropical Asian stingless bee species or in relation to anthropogenic land-use changes. Since homing distances are considered a proxy for foraging ranges (Greenleaf et al., 2007), we applied translocation experiments to estimate foraging distances in a small meliponine species (Smith et al., 2017).

Here, we firstly aimed to estimate the typical and maximum homing ranges of colonies of the tropical Asian stingless bee, *Tetragonula fuscobalteata* (Smith, 1857), located in 10 different anthropogenic landscapes. Secondly, we investigated how anthropogenic land-use affected bee homing ability. As bees are known to adjust their foraging ranges to the availability of resources provided by specific landscapes (Campbell et al., 2019; Ogilvie & Forrest, 2017), we predicted that bee homing ranges were lower for bees released in areas with high proportions of forest patches (i.e. natural habitats with high and long-seasonal resource availabilities) than for bees released in areas predominantly surrounded by agricultural and urbanised landscapes (due to restricted flowering periods and constant but patchy floral resources, respectively).

MATERIALS AND METHODS

Study species and colonies

T. fuscobalteata, a small tropical Asian stingless bee, is widely distributed in Southeast Asia and commonly kept and propagated in boxes in Thailand for honey production and pollination services (Boongird, 2011; Chuttong et al., 2016). Ten experimental colonies of *T. fuscobalteata* were prepared from 10 strong mother colonies in March 2020. To prepare each study colony, an empty wooden box (designed by Assist. Prof. Dr. Isma-ae Chelong), measuring 13 × 30 × 10 cm, was filled with a handful of pupal brood cells (34.28 ± 12.50 g, $n = 10$ hives) from one mother colony, covered with a transparent plastic sheet to enable observations and finally closed with a lid. We then smeared resin from the mother colony around the entrance hole of the new hive to attract adult bees from the mother colony (Heard, 2016). The mother colony was moved to a new place (at least 30 m away) afterwards, whilst the new colony was kept at the original site so that adult bees could return to the new colony instead of the mother hive. After approximately 4 months, 10 healthy and equally old colonies with a new queen, brood cells, nectar and pollen pots were transported to our study sites.

Study sites

The study was conducted in Songkhla and Phatthalung provinces (6°50′–7°30′N, 99°50′–100°30′E), in Southern Thailand. Both provinces are characterised by a mix of forest (14.13%), agriculture

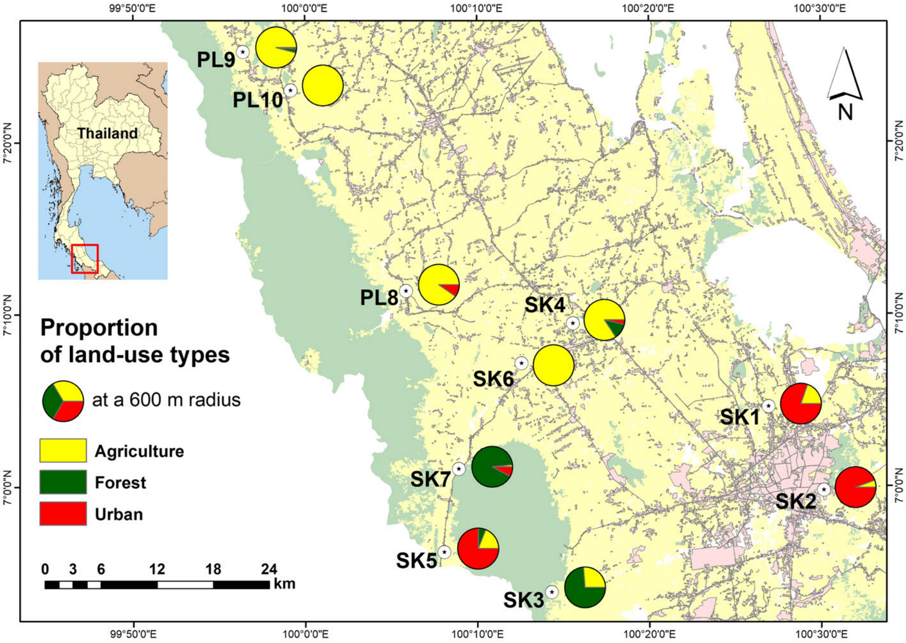

FIGURE 1 Location of experimental colonies placed in 10 mixed fruit orchards in Songkhla (SK) and Phattalung (PL) provinces, southern Thailand. Pies show the proportion of land-use types at a 600 m radius around the focal orchards

(64.38%) and urban areas (7.66%) according to the land-use data obtained for 2020 from the Land Development Department of Thailand. Forest areas composed either large tropical rainforests or smaller forest patches, whilst the majority of agricultural lands (AGs) consisted of rubber and oil palm plantations, paddy fields and orchards (Land Development Department, 2020). In the present study, we selected a total of 10 mixed fruit orchards for our colony placement, which were located along a gradient of surrounding landscape complexity (Figure 1, Table S1). These orchards included at least five cultivated fruit species (e.g., durian (*Durio zibethinus* L.), mangosteen (*Garcinia mangostana* L.), rambutan (*Nephelium lappaceum* L.), duku (*Lansium domesticum* Corr.), coconut (*Cocos nucifera* L.), mango (*Mangifera indica* L.) and longan (*Dimocarpus longan* Lour.)) and had been managed for over 10 years. The minimum distance between two orchard centres was 6.7 km. To set up an experimental colony, we placed each new colony on a PVC stand approximately 1 m above ground with the entrance facing NE (following Kaluza et al., 2016). Colonies were protected with a roof tile against direct sun and rain. All experimental colonies were kept in shaded or semi-shaded locations for 1 year before the experiment started, so that the bees could habituate to the surrounding landscapes.

Translocation experiments

We performed translocation ('homing') experiments to assess the homing ability and thus foraging distances of *T. fuscobalteata* foragers between 20 and 31 July 2021. A total of 10 colonies located in 10 different landscapes for 1 year were used. All experiments were conducted on clear sunny days, and each colony was tested once within 1 day. On each experimental day, 80 returning foragers carrying either pollen or nectar were captured at the hive entrance between 09:00 h and 11:00 h. Transparent plastic containers with a lid were used to capture returning bees. Each container lid was pierced with a needle to create several small holes and enable air flow. To capture returning bees, we closed the hive entrance with an adhesive tape. This forced returning foragers to land on instead of entering the hive and allowed us to sample foragers from the hive (Figure S1). The captured bees were subdivided into eight groups (10 each/container), and each plastic container was placed inside an ice box for 3–5 min to anaesthetise the captured bees. We then marked all bees on their thorax using acrylic paint applied with a small brush and different colours for each bee group. Once marked, we stored all bee containers inside a large cardboard box so that the bees could warm up again but could not obtain any directional (e.g., visual) information before being released. Before transporting of marked bees, we opened the hive entrance for a few seconds to allow other returning bees to enter the hive. We then closed the entrance again to ease observations and collection of returning marked bees.

Release distances were 100, 200, 300, 400, 500, 600, 700 and 800 m from each target hive. Distances and points of release were selected along the nearest road close to each hive and leading away from hives. We started with the furthest distance and moved consecutively to the shortest distance. We carried the cardboard box with marked bees to each release point by car following the selected road. Distances between release points and hives were calculated using the 'Measure distance' function in Google Maps with high-accuracy mode. For each hive, we randomly selected differently coloured groups of bees for each distance/release point. Release of all groups took place between 11:00 h and 12:00 h. To release the bees, the plastic container was opened by one observer who waited for 30 s to ensure that all bees had taken off. Bees that had not left the container until then were excluded from our experiments (which applies to 10.5% of bees). A second observer monitored the arrival of marked bees at the hive from 12:00 h to 17:00 h, captured all returning marked bees using the plastic containers and stored them in a plastic bag to prevent recounting. All bees were released after finishing the experiment. We recorded the time and colour of each returning marked bee until 5 h after release. Bees returning after 5 h were excluded from our analyses.

Surrounding landscape factors

Forest proximity (i.e., distance to the nearest forest) and the proportion of anthropogenic landscapes surrounding each study site at different radii were selected as explanatory variables. All landscape variables were measured using ArcGIS 10.5. We obtained the reference land-use map in 2020, providing the shape file data at a 1:25,000 scale and a resolution of 2.5 m digitised from satellite images, from the Land Development Department of Thailand. We defined the forest proximity as the distance between the edges of the nearest forest or forest fragment and the centre of the study site. For the anthropogenic surrounding landscape composition, we used two main land-use categories: (1) agricultural land (AG) (e.g., orchard, paddy field, perennial crop, aquacultural land, pasture and farm house) and (2) urban land (UR) (e.g., villages, city, town, factory, recreation area, institutional land, road, etc.). To take into account scale-specific responses of our study species, we calculated the proportion of each land-use type within 100, 200, 300, 400, 500 and 600 radii around the centre of our study sites (hives). The maximum distance of 600 m was based on flight ranges reported for the similarly sized Australian stingless bee species *Tetragonula carbonaria*, for which typical and maximum homing distances were estimated to be 333 and 712 m, respectively (Smith et al., 2017).

Statistical analysis

All statistical analyses were performed using the R program version 4.1.0 (R Development Core Team, 2021). We fitted a generalised linear mixed model (GLMM) using the glmer function with a binomial error distribution and a logit link function to determine the effect of distance from colony released (hereafter 'distance') on the proportion of bees that returned to the colony within 5 h (hereafter 'bee homing rate'). Hive nested within site was included as random effects. We used the function cbind() to create a binomial vector combining the numbers of successes (no. of bees returned) and the number of failures (no. of bees released minus no. of bees returned). The ggpredict function from the ggeffects package was used to predict typical and maximum homing distances of *T. fuscobalteata* as the distances at which 50% and 90% of released bees failed to return, respectively (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007; Smith et al., 2017), based on the logistic regression line. In addition, we plotted the mean (±SE) percentage of bees that returned from each release distance within 1-hour time intervals to check whether 5 h were sufficient to capture the majority of returning bees.

To determine the effect of land-use changes on bee homing ability, we initially composed a correlation matrix to identify correlations between all explanatory variables using the Hmisc package (based on Spearman's correlation tests, Table S2). Since anthropogenic landscape variables, that is, agricultural and urbanised cover, were obtained at six spatial scales, each variable was positively correlated across spatial scales, that is, larger radii included smaller radii of landscapes (Table S2). Thus, model selection was conducted for each spatial scale separately. Then, the most predictable models were compared among the six spatial scales to select the spatial scale, which best explained anthropogenic landscape effects on bee homing rate. Forest proximity was rescaled using the rescale function in the scales package. We again used the glmer function with a binomial error distribution and included hive nested within site as random factors in all candidate models. We further checked the models for multicollinearity using the check_collinearity in the performance package, which provided a variance inflation factor (VIF) value for each predictor. We did not find a VIF value more than 10, which indicates a high correlation of that predictor with other predictors. For each spatial scale, we started with the most complex model, which included distance, one landscape variable and their interaction. We then stepwise removed non-significant interactions and variables. Significance was assessed by comparing each model with a given explanatory variable/interaction to the same model without this variable using the ANOVA function in the lme4 package (based on likelihood-ratio tests and chi-square statistics). We corrected for multiple testing as a consequence of the model selection procedure by adjusting *p*-values using the false discovery rate (FDR). The model with the lowest AIC value was considered the model with the highest explanatory value. The explanatory power of these models was estimated and compared through calculating marginal and conditional R^2 with the r.squaredGLMM function in the MuMin package. The marginal R^2 represents the variance explained by the fixed effects, whilst the conditional R^2 is interpreted as the variance explained by the entire model, including both fixed and random effects (Nakagawa & Schielzeth, 2013). Moreover, a logistic regression between a significant parameter and bee homing rate was plotted with the 95% CI using the plot_model function from the sjPlot package.

RESULTS

Typical and maximum homing distances

Of 716 *T. fuscobalteata* foragers released on 10 experimental days, a total of 197 bees (27.51%) were recaptured within 5 h after releasing. A maximum of 37.18 (±6.36) % of released bees returned to their colony within 5 h (Figure 2). This proportion was highest for bees released at a 100 m distance (Figure 2). The percentage of bees that returned to each colony declined over time and approximated zero

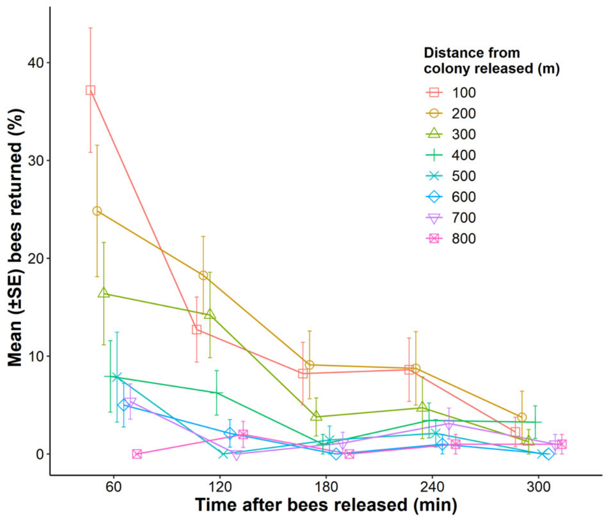

FIGURE 2 Percentage of bees returning to their colony (±SE) over 60-min time intervals. Bees were captured from 10 *Tetragonula fuscobalteata* colonies, marked and released at different distances (indicated by different symbols and colours) from the colony

after 5 h (Figure 2). This indicates that our experimental period was sufficient to recapture most returning marked foragers. Percentages of bees returning to their colonies were higher for releases at 100 and 200 m distances from the hive (accounting for 69.0 ± 5.53 and 64.7 ± 4.47, respectively) and dropped sharply between 200 and 300 m (40.4% ± 8.53% at 300 m distance) and dropped even further between 300 and 400 m (21.9% ± 4.88% at 400 m distance) (Figure S2). Using the logistic regression analysis, the typical homing distance of *T. fuscobalteata* foragers (i.e., the distance where 50% of released bees failed to return) was estimated as 240 m, and the maximum homing distance (i.e., the distance where 90% of released bees failed to return) was estimated as 595 m (Figure 3).

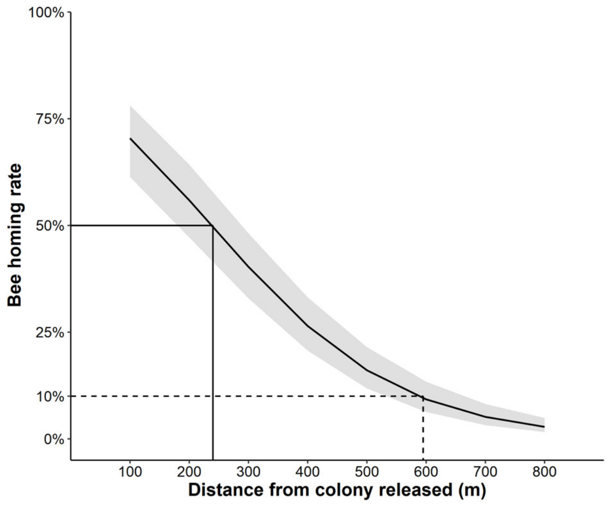

FIGURE 3 Logistic regression analysis of the proportion of bees that returned to the colony within 5 h ('bee homing rate') in relation to the released distance from colony (m). The grey shaded area represents the 95% CI, and solid and dashed lines indicate the distances where 50% and 90% of released bees did not return

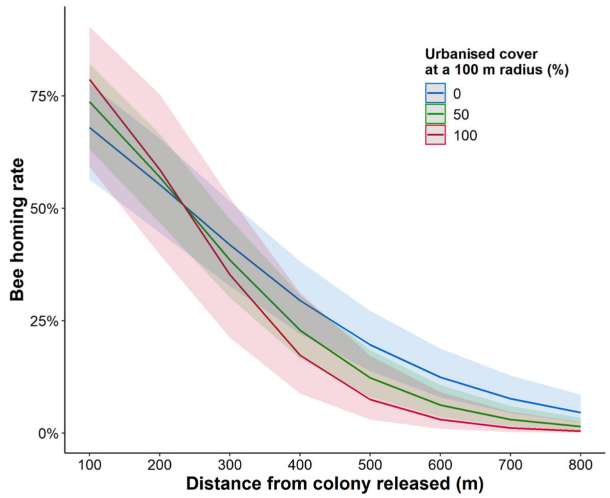

FIGURE 4 Bee homing rates were significantly affected by an interaction between release distances from colonies and the proportion of urbanised area within a 100 m radius around colonies. Shaded areas represent 95% CIs for each logistic regression line

Effects of surrounding landscape on bee homing ability

Bee homing rates were best described by the model including release distance from colony, and its interactions with the proportion of urbanised cover at a 100 m radius (Table S3). We found that release distance had a strong negative effect on bee homing rates (GLMM: $\chi^2 = 199.58$, d.f. $= 1$, $p < 0.001$), whereas the proportion of urbanised cover at a 100 m radius alone did not affect bee homing (GLMM: $\chi^2 = 0.7172$, d.f. $= 1$, $p = 0.397$). Bee homing correlated negatively with release distance, and the drop was most pronounced for colonies placed in areas with high proportions of urbanised land within a 100 m radius (GLMM: $\chi^2 = 6.0274$, d.f. $= 1$, $p = 0.014$, Figure 4). Forest proximity and proportion of agriculture and urban cover within 100, 200, 300, 400, 500 and 600 m radii did not affect bee homing rates (Table S3).

DISCUSSION

Typical and maximum homing distances

According to our homing experiments, we find the typical and maximum foraging distances of an economically important tropical Asian stingless bee species, *T. fuscobalteata*, to be 240 and 595 m, respectively. In the previous study, Smith et al. (2017) reported the typical and maximum foraging ranges for the Australian stingless bee *T. carbonaria* to be 333 and 712 m, respectively. Interestingly, the formulae suggested by Greenleaf et al. (2007) based on IT span (1.2 mm for *T. fuscobalteata*, Wayo et al., 2020) predicted the typical and maximum homing distances of this species to be 41 and 80 m, respectively. Our results thus show that predictions based on IT span may underestimate homing distances in stingless bees, as also found by other studies (Campbell et al., 2019; Smith et al., 2017). This discrepancy may be explained by resources being more patchily distributed in real landscapes than predicted for optimal foraging situations. Future work should test the effect of body size on foraging ranges in stingless bees. For instance, stingless bee colonies of *Melipona mandacaia* with larger foragers collected food (from a feeder) across larger distances than colonies with smaller foragers (Kuhn-Neto et al., 2009). Moreover, estimates based on IT span cannot account for the complex communication system of stingless bees, which enables foragers to communicate even distant locations of (food) sources (Barth et al., 2008; Nieh, 2004).

As expected, there homing rates declined with increasing release distance, which has also been observed for other stingless bee species (Campbell et al., 2019; Silva et al., 2014; Smith et al., 2017). In fact, percentages of *T. fuscobalteata* returning to their colonies were relatively high at distances up to 200 m but decreased sharply thereafter, indicating that foragers were most familiar with the landscapes within a 200 radius around their hives. Honey bees, *Apis mellifera*, typically explore novel sectors of their foraging terrain during consecutive orientation flights and start foraging flights after orientation flights have covered greater distances (Degen et al., 2015). Consequently, honey bee homing flights were faster and straighter when honey bees were released within the explored area than outside (Degen et al., 2016). Assuming that stingless bees apply a similar strategy to familiarise themselves with their foraging landscape, this may explain why navigational skills of our study bees were good within 200 m. In contrast, surrounding areas at distances greater than approximately 600 m had likely not been previously explored by the released bees and were thus less familiar to them, resulting in lower homing abilities at further distances. We can of course not rule out that typical and maximum foraging distances will change over the course of the year as a consequence of seasonal changes in resource distribution and availability.

Landscape effects on bee homing ability

In contrast to our expectations, forest proximity and surrounding landscape composition within 100, 200, 300, 400, 500 and 600 m radii did not affect bee homing rate. This may be a consequence of our study landscapes providing similar resource availabilities for *T. fuscobalteata* at the time of the study period. However, homing ranges of stingless bees vary over the season (Campbell et al., 2019), suggesting that homing distances of *T. fuscobalteata* should be studied in different seasons, ideally in relation to available floral resources, to fully capture landscape-related variation in foraging distances in this species. Notably, we found a significant interaction between release distances from colony and the proportion of urbanised cover at a 100 m radius, that is, the effect of urbanisation on bee homing rate depended on the release distance. When bees were released within the typical homing range (240 m), more bees returned to colonies placed in areas with higher proportions of urbanised land than to colonies placed in areas with lower proportions of urbanised land. On the other hand, when bees were released outside of their typical homing/foraging range, less bees returned to colonies placed in areas with higher proportions of urbanised land than to colonies placed in areas with lower proportions of urbanised land. This effect of the urban landscape may be explained by the constant and/or abundant (food) resources provided in, for example, urban or suburban gardens, home gardens and backyards in the urbanised landscapes of Southern Thailand. With more (food) resources available close to the colonies, the bees may have explored and familiarised themselves with a smaller foraging range around their nests, resulting in an overall better knowledge of the surrounding landscape. Our results thus agree with previous findings showing that urban gardens provided higher flowering species richness than natural areas across seasons (Kaluza et al., 2016; Marín et al., 2020), which greatly increased population growth of stingless bees due to a continuous supply of floral resources (Kaluza et al., 2018). Besides resource abundance, urbanisation associated with spatial aggregation of resources, coarse/fine structure of landscape and costs of travelling and searching may influence bee homing range.

Conservation implications

Our findings indicate that small stingless bee species are able to forage in different anthropogenic landscapes beyond distances predicted by their body size. Moreover, bees appear to adjust foraging distances to the distribution and availability of (food) resources in the landscape surrounding their nest. This knowledge is crucial for developing landscape management strategies that support wild and managed stingless bee colonies and to mitigate further loss of pollination services in anthropogenic landscapes. Since stingless bees are vital pollinators for many crops, knowledge on the actual species-specific maximum homing distances is important, for example, for pollinator management at farms. For example, the small foraging distances of *T. fuscobalteata* observed at resource-rich landscapes render this species suitable for greenhouse pollination and target crop pollination as foragers will likely focus mainly on target crop flowers within nest proximity rather than other flowers at further distances in adjacent areas (Smith et al., 2017). In fact, *T. fuscobalteata* can nest in both natural and anthropogenic landscapes and can be reared in wooden boxes for honey production and pollination services (Chuttong et al., 2014). However, as stingless bees are known to rely on a diversity of floral resources to sustain their colonies throughout seasons (Kaluza et al., 2018), farmers also need to ensure to provide sufficient and diverse floral resources in or close to fields (i.e., within maximum homing range) in particular in human-modified landscapes in order to support this species in periods without flowering crops.

In fact, our estimates for homing distances have important implications for stingless bee conservation. As resource-rich tropical rainforest patches are key habitats for natural nesting and foraging, forest areas should be preserved in vicinity to crop areas to provide both natural pollinators for crops and food sources for managed pollinators.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Permission to work with the animals of this research project (project number 2562-01-073) was granted by Institutional Animal Care and Use Committee, Prince of Songkla University.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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

Table S1. Location of study sites and geographic information.

Table S2. Spearman correlations with forest proximity and proportion of land-use types.

Table S3. Model selection process following a step-wise procedure.

Figure S1. Using a transparent plastic container to capture returning bees.

Figure S2. Percentage of bees returning within 5 h at different distances from the colony.

Appendix S1. Data used in Wayo et al. 'Homing ability in a tropical Asian stingless bee is influenced by interaction between release distances and urbanisation'.

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