Temporal variation in homing ability of the neotropical stingless bee Scaptotrigona aff. postica (Hymenoptera: Apidae: Meliponini)

Alistair John Campbell, Rafael Leandro Corrêa Gomes, Karoline Chaves da Silva, Felipe Andrés León Contrera

Original article

Temporal variation in homing ability of the neotropical stingless bee *Scaptotrigona* aff. *postica* (Hymenoptera: Apidae: Meliponini)

Alistair John CAMPBELL[1,2], Rafael Leandro Corrêa GOMES[1], Karoline Chaves da SILVA[1], Felipe Andrés León CONTRERA[1]

[1]Laboratório de Biologia e Ecologia de Abelhas, Universidade Federal do Pará, Instituto de Ciências Biológicas, Rua Augusto Corrêa, No 1, Campus Básico, Guamá, Belém, PA 66075-110, Brazil
[2]Departamento de Entomologia, Embrapa Amazônia Oriental, Belém, Pará 66095-903, Brazil

Abstract – Body size is a known predictor of foraging distance in stingless bees (Apidae: Meliponini). However, effects of seasonality on foraging distances, particularly in tropical regions, are poorly understood. Here, we use translocation ('homing') experiments, the release of marked individuals at various distances from the nest, to investigate how homing abilities of the Neotropical stingless bee, *Scaptotrigona* aff. *postica* differ across the transition between wet and dry seasons (February–August) in a heterogenous tropical landscape in the eastern Brazilian Amazon. We also determined nectar sugar concentrations of unmanipulated returning foragers to assess temporal changes in collected resource quality. Maximum and typical homing distances (i.e. distances where 90% and 50% of released bees are lost) were estimated to be 860 and 392 m, respectively, confirming that while some individuals travel long distances, most workers must remain close to nests during foraging trips. Homing distances and collected nectar sugar concentrations showed inverse temporal patterns, as homing range declined in later months (May to August), whereas nectar sugar concentrations increased over the same period. Thus, shorter homing distances in later 'dry season' months probably reflected an increased availability of floral resources compared with earlier months. Together, our findings highlight the limited spatial extent of foraging activities in *S.* aff. *postica* workers, and that bee homing distances vary with environmental conditions. These results provide useful information for both stingless bee colony management and conservation in humid tropical regions.

foraging range / stingless bees / Amazon rainforest / translocation experiment / tropical pollinators

1. INTRODUCTION

Bees are important animal pollinators of both wild and cultivated plant species (Klein et al. 2007; Ballantyne et al. 2017). However, both wild and managed bee populations are threatened by factors associated with human activities, including land use change, agrochemical use, novel pests and pathogens, exotic species invasions and climate change (Vanbergen 2013). As all bees are central-placed foragers (i.e. nest-dwelling), they must have access to all required resources for their survival and reproduction (e.g. pollen, nectar, water, resins) within their maximum foraging range, i.e. the maximum distance from the nest that individuals can travel. This makes bees highly sensitive to the loss of diverse natural or semi-natural vegetation (e.g. forests, unimproved grasslands) when compared with other insect pollinator taxa, such as flies or beetles (Rader et al. 2016). Therefore, understanding how bees use and move

Corresponding author: A. Campbell,
alistaircampbell87@googlemail.com
Manuscript editor: Alexandra Klein

through space around their nests is critical to avoid further population declines and loss of ecosystem functioning (Greenleaf et al. 2007).

Bee species' foraging distances have been shown to be a function of body size as measured by intertegular distance (ITD), a robust predictor of overall body mass, where larger species fly disproportionately greater distances from the nest than smaller species (Cane 1987; Greenleaf et al. 2007). However, important resources for bees (e.g. pollen, nectar) are patchily distributed throughout landscapes, being largely determined by environmental conditions, such as landscape composition and seasonal changes in flower abundance (Wiens et al. 1993). To deal with this variability, bees optimize their foraging activities, i.e. where distant patches are only visited if patch quality, minus energy expended in flight (outbound and inbound), exceeds that of closer patches (Charnov 1976). Accordingly, few individuals travel distances approximating species-specific maximum foraging distances (Zurbuchen et al. 2010), and typical flight distances are usually much shorter and often correlate with environmental conditions. For example, studies on the 'waggle dance' of workers of the Western honeybee (*Apis mellifera*) have shown that flight distances increase in simplified landscapes (i.e. dominated by intensive agriculture), and during periods of resource scarcity (e.g. late summer) (Steffan-Dewenter and Kuhn 2003; Couvillon et al. 2014). Likewise, bumblebees and stingless bees undertake shorter foraging trips (in terms of duration) in high-quality landscapes compared with low-quality landscapes (Westphal et al. 2006; Leonhardt et al. 2016). Therefore, species-specific foraging distances may vary considerably in both space (i.e. different landscapes) and time (i.e. seasonality). However, most studies on bee foraging distances occur over short time periods, and therefore may represent only 'snapshots' of total variation in foraging distances. Thus, information gathered over longer time periods can provide more robust estimates of bee foraging distances, and from an applied perspective, identify "dearth periods" for bees, when additional forage or supplementary feeding would be most beneficial.

In the tropics, stingless bees are the dominant eusocial bees and are represented by over 400 species in the neotropical region alone (Pedro et al. 2014). They are essential pollinators in these regions (Bawa 1990; Giannini et al. 2015) and are increasingly managed for crop pollination, honey production and other products (e.g. stored pollen, resin) (Cortopassi-Laurino et al. 2006; Slaa et al. 2006). All stingless bees live in perennial colonies, and apart from a few necrophagous species, must collect pollen and nectar year round to maintain their populations (Marques-Souza et al. 2007; Aleixo et al. 2017). As with other eusocial bees (honeybees, bumblebees), stingless bees assimilate information from a variety of celestial and terrestrial cues (e.g. landmarks, polarized light, magnetic fields) to navigate through landscapes (Michener 2007) and have evolved several sophisticated mechanisms by which to communicate the location of rewarding food patches to nestmates (Leonhardt 2017). In particular, several stingless bee genera (including *Scaptotrigona* species) use 'polarized' odour trails, where returning workers deposit chemical markers (labial gland secretions) with increased frequency in close proximity to the targeted resource so that other foragers can quickly find and exploit it (Nieh 2004; Jarau 2009). However, unlike honeybees, intranidal communications either do not exist, are not location specific, or have as yet not been described sufficiently to enable inference of foraging locations (Nieh 2004; Hrncir and Maia-Silva 2013).

Previous experiments on foraging distances in stingless bees have predominantly used either artificial feeders, where workers are trained to feed on and recruit to nectar feeders placed at increasing distance from the nest (Kuhn-Neto et al. 2009; Silva et al. 2014) or translocation ('homing') experiments, where captured bees are released at increasing distance from the nest (Roubik and Aluja 1983; Smith et al. 2017). Results from these experiments demonstrate that 'maximum homing distances' in stingless bees are, as in other bee taxa, a function of overall body size (van Nieuwstadt and Ruano Iraheta 1996; Araújo et al. 2004; Kuhn-Neto et al. 2009). However, maximum homing distances are known for only a small number of total stingless bee genera and species and may not reflect typical flight distances, due to optimal foraging behaviour, or

account for effects of seasonality (e.g. wet vs dry season) on flight distances. Moreover, increased pressure on wild populations from human activities (e.g. deforestation) (Brown and De Oliveira 2014) and growing interest in the use of managed hives to improve crop pollination (Jaffé et al. 2015) strengthen the need to understand spatiotemporal dynamics of foraging in stingless bees, particularly in understudied regions such as the Brazilian Amazon.

Here, we use translocation experiments to investigate homing ability of the neotropical stingless bee, *Scaptotrigona* aff. *postica*, and how homing distance varies over the transition between Amazonian wet and dry seasons (February to August). We also determine nectar sugar concentration, which correlates with resource quality, of returning workers. Specifically, we asked (1) what are the typical and maximum homing distances of *S.* aff. *postica*? (2) Do homing distances vary over the transition period between wet and dry seasons? And (3) How does resource quality (nectar sugar concentration) vary over the transition period between wet and dry seasons?

2. MATERIALS AND METHODS

2.1. Study species

The neotropical bee species, *Scaptotrigona* aff. *postica*, known locally as "abelha canudo" ("straw bee"), due to its characteristic tubular nest entrance (Leão et al. 2016), is found throughout Brazil, Bolivia and Peru (Camargo and Pedro 2013; Pedro et al. 2014). It is commonly kept by Brazilian beekeepers due to its ease of management, populous colonies (c. 15,000 adult bees), excellent honey production and potential use in crop pollination (Jaffé et al. 2015; Leão et al. 2016). Workers visit a diverse array of flowering plant species (60–97 species; Marques-Souza et al. 2007; Aleixo et al. 2017) and recruit nestmates to rewarding food patches using complete 'polarised' odour trails, which become more intense close to the identified food source (Kerr et al. 1963; Nieh 2004). Maximum homing distance was estimated by Araújo et al. (2004) to be 1700 m, based on a linear regression of wing length and maximum homing distances of six

non-congener species, whereas estimates based on Greenleaf et al. formula with ITD (1.7 mm, Cabral et al., *unpubl. data*) predict typical and maximum homing distances of 127 and 258 m, respectively (Greenleaf et al. 2007).

2.2. Study site

The experiment was conducted from February to August 2017 at the meliponary of the Botany department, Embrapa Amazônia Oriental, Belém, Pará state, Brazil (1°26′11.52″S, 48°26′35.50″W). The study landscape is characterised by large areas of tropical rainforest and urban land uses (Belém), with the meliponary located at the intersection of these two distinct land uses (Figure 1). The first 500 m from the meliponary in all directions except north (300-m extension) remains within the grounds of Embrapa Amazônia Oriental, which constitute a mixture of secondary forest, agroforestry crops (e.g. açaí palm, *Euterpe oleracea* Mart., cupuaçu, *Theobroma grandifolia* (Willd. ex Spreng.) K. Schum), herbaceous vegetation and amenity grassland. In general, urban areas contain few, sparsely distributed parklands and green spaces, with few large trees (mainly the exotic *Mangifera indica* L.).

The region's climate type is considered as *Af* tropical rainforest according to the updated Köppen classification (Peel et al. 2007). Mean monthly temperatures are stable between 25 and 26 °C; and mean monthly rainfall varies between a maximum of 447 mm in March and a minimum of 115 mm in October (INMET 2019). Accordingly, we considered the study period to encapsulate the transition between wet (November to April) and dry (May to October) seasons in the Amazon region.

2.3. Translocation experiments

We used translocation ('homing') experiments, the experimental release and recapture of foragers at different distances from the nest, to assess homing ability of *S.* aff. *postica* workers. Many authors consider homing ability as a good proxy of actual foraging distances in bees, but with several important caveats. Firstly, translocation experiments do not directly measure foraging, rather
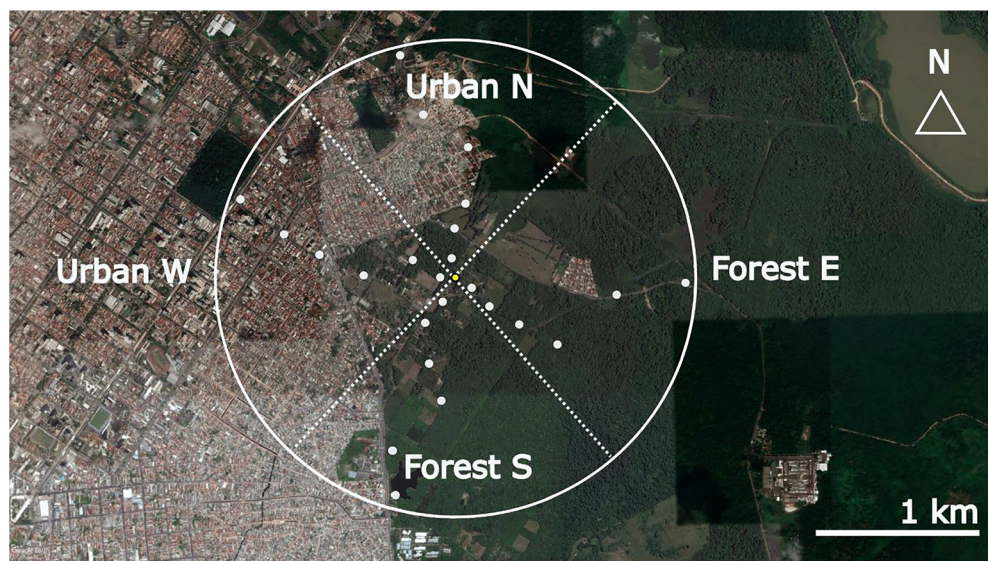
Figure 1. Map of study landscape (experimental colonies located at centre) with area within predicted maximum foraging radii (1500 m) divided into four segments: areas dominated by urban land uses (Urban N and Urban W); areas dominated by forested habitat (Forest E and Forest S); and release points (100, 300, 500, 800, 1000, and 1500 m away from colonies; filled white circles) within each segment.

the capacity of individuals/species to relocate the nest, based on flight ability, physiology (e.g. energy stores), weather conditions and environmental cues (e.g. landmarks, other foragers, odour trails) (Greenleaf et al. 2007). Secondly, they do not account for energy expended during outbound flights, and so may overestimate actual foraging distances. Equally, as resource-rich habitats are patchily distributed in landscapes, translocation experiments may sometimes underestimate foraging distances if release points are situated in unfamiliar habitats. In other bees, use of radio tracking devices (larger species) (Pasquet et al. 2008; Pahl et al. 2011), manipulation of host plant location (diet specialists) (Zurbuchen et al. 2010) and/or interpretation of intranidal communications (honeybees) (Couvillon et al. 2014) can overcome some of these limitations. Nevertheless, despite these problems, translocation experiments can provide meaningful data on flight distances in small, generalist bee species that lack sophisticated intranidal communication mechanisms (Smith et al. 2017).

Based on a previously published estimate of maximum homing distance for *S*. aff. *postica* workers (Araújo et al. 2004), a circle with a radius

of 1.5 km was defined around the meliponary in Google Earth Pro (Google Inc., version 7.3.1) (Figure 1). To evenly sample surrounding habitats, this area was divided into four equal segments, based on cardinal directions and habitat type, with two areas dominated by urban dwellings (Urban North and Urban West) and two areas dominated by tropical rainforest (Forest East and Forest South) (Figure 1). Within each segment, we selected release points at six distances away from the colonies (100, 300, 500, 800, 1000 and 1500 m; Figure 1). All 24 release points were selected along roads or forest trails where access permitted release of captured bees.

A total of five colonies of *S*. aff. *postica* housed in vertical hives were selected for use in the experiment. Colonies were considered in good condition based on standardised assessment procedures (i.e. external activity, entrance tube size, brood comb area and presence of food stocks) (Leão et al. 2016). Colonies were fed twice monthly with 30 ml sugar syrup (60%) in periods outside of experimental data collection. Each month, all colonies were evaluated and the three strongest colonies (based on comparison of the above criteria) were selected for use in experiments to avoid

excessive worker mortality in weaker colonies. We were unable to collect data in June due to restricted access to colonies after a large tree fell within the meliponary. Translocation experiments took place over 6 days each month, with a maximum number of three consecutive study days to minimise possible confounding effects of repeated sampling methods on bee recapture rates.

Each study day, we captured 40 bees from experimental colonies between 0800 and 1000 h, prioritising capture of returning foragers (i.e. pollen loads or full nectar crops). Following capture, bees were subdivided into groups of ten nestmates and marked with non-toxic paint on the thorax to identify colony and release point. We released groups of workers at four points each day, with no two points at the same distance from the hive or in the same landscape segment (e.g. Forest East 100 m; Forest South 300 m; Urban North 500 m; Urban West 800 m). Paint colours were rotated among colonies to ensure that each colour was used once every three study days, and release point order was randomised to avoid any confounding effects of sampling order. Marked bees were placed in closed Petri dishes under controlled conditions (26 °C), with ad libitum access to sugar syrup (60%), before being transported (maximum of 1 h captivity in Petri dishes to avoid heat stress) to release points in a cardboard box to deprive workers of any distance or directional information from the surrounding landscape about the release point in relation to the hive (Pahl et al. 2011).

Prior to the release of marked bees, hives were closed for a second time, rotated 180° on their vertical axis, and a piece of cerumen (beeswax; Roubik, 1989) placed where the entrance was previously to attract returning workers and facilitate their collection. Upon their release, any worker that had damaged wings or did not fly off within 15 s of opening the Petri dish was killed and subsequently excluded from analyses. Individual colonies were then observed to collect returning bees until 90 min had elapsed following the last release point. Bees returning after 90 min were collected but excluded from our analyses. All experiments were performed on days with stable weather conditions (i.e. wind speed < 6 km/h, sunny), and at least 24 h after heavy rain to ensure bees had been foraging

normally on the previous day. Temperature (°C) and relative humidity (%) were recorded at midday using a thermohygrometer.

2.4. Nectar sugar concentration

To investigate seasonal changes in resource quality available to foragers, on three non-consecutive days each month, five 'unmarked' workers (not included in translocation experiments) returning with full nectar crops were caught and forced to regurgitate some the stored nectar onto the surface of a handheld refractometer (Bellingham and Stanley Ltd., Tunbridge Wells, Kent, UK). Readings show total sugar concentration (% w/w, °Brix) of the sampled material (up to 45%) and readings of 0% indicated the examined individual had been collecting water.

2.5. Statistical methods

To ensure that 90 min was sufficient to recapture all returning bees, we regressed the mean number of bees returning against time taken (divided into six 15-min intervals) to determine the time at which no bees would return. We compared residual standard errors (S) for models constructed using both linear and non-linear regression terms (R functions lm and nls). The regression model with the lowest residual standard error was considered the best fit of our data.

To define typical and maximum homing distances of S. aff. postica workers (question 1) and temporal variation in homing range (question 2), we used generalised linear mixed effects models (GLMMs) with binomial error distributions in the R package 'lme4' (Bates et al. 2015). We defined typical and maximum homing distances as the 50th and 90th percentiles of logistic regression lines, i.e. translocation distances at which 50% and 90% of released bees were lost (Gathmann and Tscharntke 2002; Smith et al. 2017). The response variable was the proportion of released workers returning in 90 min ('bee return rate'). Fixed effects included distance from nest (herein 'distance'), sampling month, temperature, relative humidity and the two-way interaction between distance and sampling month. To test whether

temporal patterns in bee return rates were explained by changes in resource quality, we additionally ran models with mean monthly nectar sugar concentration in place of sampling month. To account for the nested design and repeated measures, colony was included as a random effect. Prior to model selection, all fixed effects were checked for collinearity to exclude models with high levels of collinearity between included predictors using the function 'max.r' (https://github.com/rojaff/dredge_mc). Best models were selected by comparing Akaike information criterion (AIC) values of all possible models using the dredge function in the R package 'MuMIn' (Barton 2015). Significance of predictors included in selected models was tested using Wald tests (Z).

To test the effect of month, temperature and humidity (recorded at midday) on nectar sugar concentration, we used linear mixed effects models using R package 'nlme' (Pinheiro et al. 2016). Colony was included as a random effect to account for repeated measures design. Best-fitting models were selected from all viable models using same procedure reported for bee return models. We compared only simple models (single predictor) as fixed effects were highly correlated. All full and final models were visually checked for homogeneity of variance and normality of residuals and graphs produced in R (R Core Team 2017).

3. RESULTS

A total of 4187 bees were released in 426 separate trials. Of these, 1407 (33%) were subsequently recaptured at colony entrances within 90 min. The mean number of bees returning within discrete 15-min intervals after release was best explained by a non-linear regression model (linear: S = 0.05, d.f. = 4; non-linear: S = 0.04, d.f. = 3), that followed a negative sigmoidal curve, dropping below 0.05 bees/15 min^{-1} after 120 min, before eventually asymptoting at < 0.01 bees after 155 min (Figure 2a), suggesting that 90 min was sufficient to recapture most released bees that successfully relocated the colony.

3.1. *Typical and maximum homing distances in S.* **aff.** *postica* **workers**

Translocation distance from nest was included in the best fitting model of worker return rates (Table I), having a strong negative effect on the proportion of released bees that returned ($Z = -11.59$, $P < 0.001$). We estimated typical and maximum homing distances (± 95% confidence intervals) for S. aff. *postica* workers of 392 ± 17 and 860 ± 27 m, respectively (Figure 2b).

3.2. *Temporal variation in S.* **aff.** *postica* *workers' homing distances*

The best fitting model of bee return rates included translocation distance, sampling month, and two-way interaction between distance and month (Table I). Typical and maximum homing distances of S. aff. *postica* workers varied greatly between sampling months, being the highest in the first 2 months (February and March) (Table II; Figure 3). Temporal changes in bee homing distances broadly mirrored shifts in abiotic conditions (temperature, relative humidity) that took place during the experiment, reflecting the transition between Amazonian wet and dry seasons, although the lowest maximum homing distance was reported in April (666 m), at the end of the rainy season (Table II). However, models including mean monthly nectar sugar concentration (see results, Sect. 3.3) in place of sampling month did not significantly improve variance explained by fixed effects (ΔAIC = 112.11).

3.3. Nectar sugar concentration

Sampling month, rather than abiotic condition (temperature, humidity), best explained variation in nectar sugar concentration collected from returning workers ($Z = 100.38$, $P < 0.001$; Table III). Nectar sugar concentrations collected by workers were approximately 50% lower during the first 3 months of the experiment compared with the latter 3 months (Figure 4).
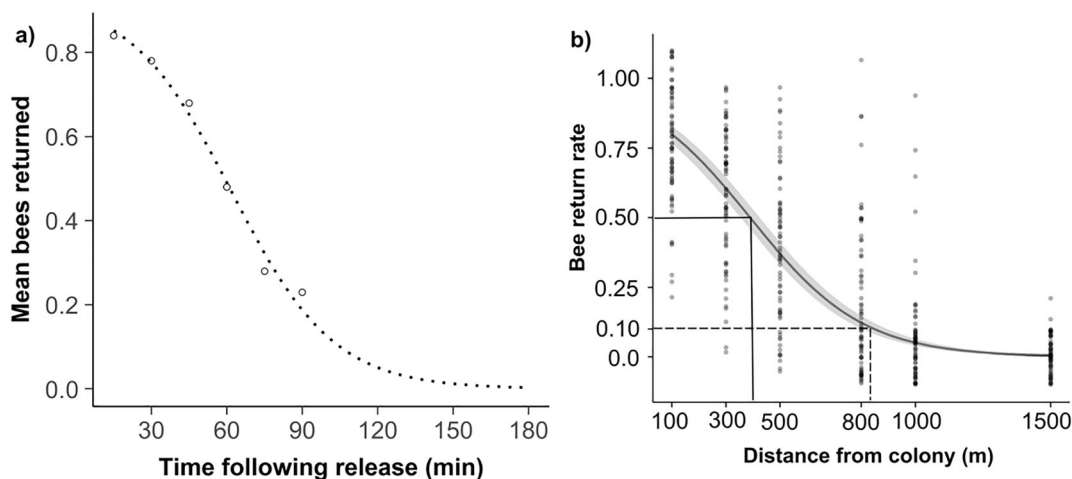
Figure 2. Mean number of individual bees collected as a function of time following release (15 min intervals). Dotted black line represents prediction based on non-linear regression model (**a**); **b** logistic regression analysis of the proportion of bees that returned to the colony within 90 min ('bee return rate') as a function of translocation distance (in metres). Grey ribbons represent 95% confidence intervals, and solid and dashed lines indicate translocation distances of 50% and 90% probability of loss of released bees (i.e., typical and maximum foraging distances), respectively.

4. DISCUSSION

Knowledge on how bees use and move through space (i.e. foraging range) and their response to anthropogenic disturbance is essential for the maintenance of bee diversity and global pollination services (Greenleaf et al. 2007). However, much of the existing knowledge on this topic is from temperate regions, limiting its applicability to other global regions (Archer et al. 2014). Here, we used translocation experiments to determine typical and maximum homing distances of an economically important neotropical stingless bee species, *Scaptotrigona* aff. *postica* , and how homing distances vary over time. We found that maximum homing distance of *S.* aff. *postica* workers was an intermediary of two previous estimates based on morphological attributes (wing length, ITD) (Araújo et al. 2004; Greenleaf et al. 2007), and that homing distances gradually decreased over the transition period between Amazonian wet and dry seasons. However, typical homing distances (i.e. distance where 50% of bees were lost) were consistently less than half those of maximum homing distances. We use our findings to discuss the validity of using maximum foraging

distances in conservation planning and their applications for meliponiculture and crop pollination in the Amazon region.

Bee foraging ranges are predicted to be a function of body size; however, species-specific estimates vary greatly between published studies and sampling methodologies (Roubik and Aluja 1983; van Nieuwstadt and Ruano Iraheta 1996; Araújo et al. 2004; Greenleaf et al. 2007). For example, formulae presented in Greenleaf et al. (2007) predicted a maximum homing distance for *S.* aff. *postica* workers of 260 m, based on ITD. In contrast, Araújo et al. (2004) predicted a maximum homing distance of 1700 m, based on a generalised measure of wing length in six non-*Scaptotrigona* species (predominantly larger-bodied *Melipona* species). Our maximum homing distance estimate of 860 m shows that predictions based on ITD may underestimate maximum homing distances in stingless bees, as found for other bee taxa (Zurbuchen et al. 2010). This may be because ITD estimates do not account for the complex communication mechanisms that have arisen within this group (e.g. odour trails, group foraging behaviours, intranidal communications), which allow workers to travel further by reducing

Table I. Effects of translocation distance (m), sampling month (February to August) and the two-way interaction term on the proportion of bees that returned to colonies ('bee return rate'). Table shows parameter estimates, standard errors, Wald (Z) test values and P values (alpha = 0.05) of fixed effects included in best model of binomial GLMM analyses. Reference value (intercept) is predicted bee return rate (logit transformed) at nest entrance (0 m) in February

Fixed effect	Estimate	St. error	Z	P
Intercept	1.383	0.180	7.68	< 0.001
Distance	− 0.003	0.000	− 11.59	< 0.001
March	0.661	0.247	2.68	0.007
April	0.975	0.287	3.40	< 0.001
May	0.184	0.264	0.70	0.487
July[a]	0.271	0.260	1.04	0.296
August	0.630	0.258	2.44	0.015
Distance: March	− 0.001	0.000	− 1.88	0.060
Distance: April	− 0.004	0.001	− 6.39	< 0.001
Distance: May	− 0.003	0.001	− 4.68	< 0.001
Distance: July	− 0.002	0.000	− 4.24	< 0.001
Distance: August	− 0.002	0.000	− 4.05	< 0.001

[a] Experiments were not conducted during June 2017 (see Sect. 2.3)

energy spent actively searching for resource patches (Nieh 2004; Hrncir and Maia-Silva 2013). However, it is important to note that as homing experiments do not directly measure foraging activity, rather the capacity of released bees to relocate the nest based on cues from the surrounding landscape and nestmates (e.g. odour trails), or account for energy expended during outbound flights, our findings probably to some degree overestimate actual foraging distances. Although we tried to replicate conditions experienced by foragers 'in the field' by selecting only workers returning with pollen loads or nectar crops (i.e. individuals with at least some previous foraging experience).

On the other hand, while the estimate of maximum homing distance presented by Araújo et al. (2004) was credible (1% bee return rate at 1500

Table II. Mean, minimum, and maximum values of daily temperature (°C) and relative humidity (%), colonies used, number of releases, and typical and maximum foraging distances of S. aff. postica workers in each sampling month

Month	Temperature (°C)			Humidity (%)			Colonies	N	Dist. (m)	
	Mean	Min.	Max.	Mean	Min.	Max.			Typical	Max.
February	29.3	28.8	29.9	82.0	81.0	84.0	II, III, IV	72	481.81	1217.17
March	30.1	28.7	31.7	76.6	73.0	79.0	I, II, III, IV	72	566.67	1160.61
April	31.1	30.2	32.2	79.3	74.0	87.0	I, II, IV	72	340.40	665.65
May	33.0	29.0	36.8	67.6	57.0	77.0	I, II, IV	67	283.84	679.80
July[a]	33.0	32.0	33.7	64.0	55.0	78.0	I, IV, V	72	340.40	778.79
August	34.0	33.3	34.8	57.3	55.0	59.0	I, II, IV, V	71	425.25	891.92
Overall								426	392.40	860.00

[a] Experiments were not conducted during June 2017 (see Sect, 2.3)
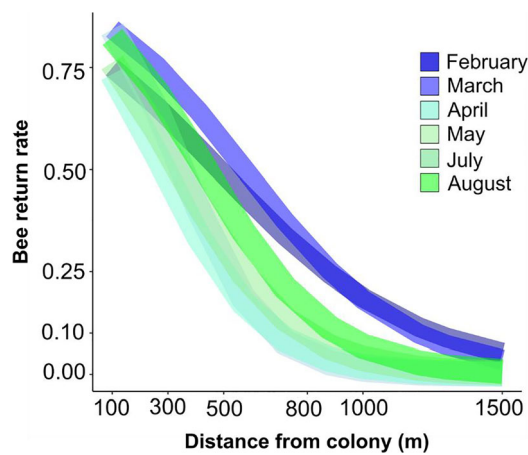
Figure 3. Temporal variation in homing range of *S.* aff. *postica* workers: proportion of bees that successfully returned to the colony within 90 min ('bee return rate') as a function of translocation distance from the colony (in metres) in different sampling months (February to August). Thickness of regression lines is representative of 95% confidence intervals (for model details, see Table I).

approximation of the actual area requirements of *S.* aff. *postica* colonies. Instead, we suggest the use of lower threshold distances, for example the distance at which 50% of individuals return, to be a more useful means to define bee species' area requirements (Zurbuchen et al. 2010). In this example, priorities for *S.* aff. *postica* colonies would be any flower-rich habitats within a 400-m radius. This finding also has important applications for crop pollination programs involving *S.* aff. *postica*, defining the likely 'area of influence' within crop fields. While this distance is considerably smaller than typical foraging distances in honeybees (1–2 km; Couvillon et al. 2014), alongside the advantages of using a native pollinator over an exotic species, a smaller foraging radius increases the likelihood that workers will visit target crop flowers, rather than those in adjacent habitats (Smith et al. 2017).

m), it was approximately two times larger than our estimate (860 m), and therefore most likely a poor

Temporal variation in homing distances of *S.* aff. *postica* workers coincided with changes in collected nectar resource quality, being larger in periods of low resource quality and smaller in periods of high resource quality. Collected

Table III. Effects of sampling month (February to August), temperature (°C), and relative humidity (%) on nectar sugar concentration collected from *S.* aff. *postica* workers. Table includes parameter estimates, standard errors, *t* test values, and *P* values (alpha = 0.05) of fixed effects included in all tested models. Only simple models were tested due to collinearity between fixed effects. Abiotic variables (temperature and humidity) were recorded at midday on each collection date. Only the first model was selected (ΔAIC < 2)

Fixed effect	Estimate	St. error	*t* value	*P*	AIC	ΔAIC
Model 1					1949.81	0.00
(Intercept)	27.80	1.42	19.56	< 0.001		
March	− 4.29	2.01	− 2.13	0.034		
April	− 1.31	2.01	− 0.65	0.515		
May	9.92	2.02	4.90	< 0.001		
July[a]	11.36	2.07	5.48	< 0.001		
August	12.81	2.01	6.37	< 0.001		
Model 2					1975.65	25.84
(Intercept)	72.16	4.28	16.87	< 0.001		
Humidity (%)	− 0.56	0.06	− 9.39	< 0.001		
Model 3					2001.64	51.83
(Intercept)	− 33.22	9.35	− 3.55	< 0.001		
Temperature (°C)	2.08	0.29	7.07	< 0.001		

[a] Experiments were not conducted during June 2017 (see Sect. 2.3)
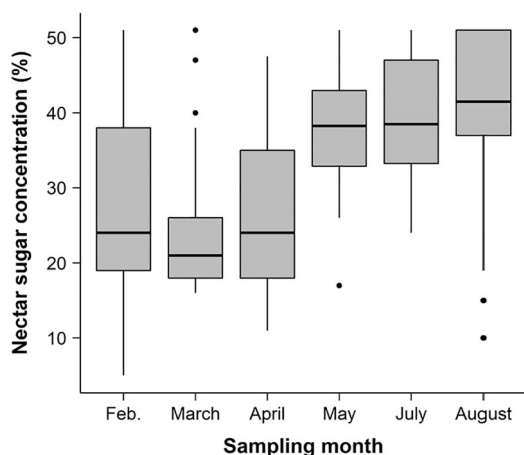
Figure 4. Median nectar sugar concentration of collected *S.* aff. *postica* workers in different sampling months (February to August). Bold horizontal lines indicate median values, grey boxes represent interquartile range, and lines and dots indicate range and outliers.

resource quality often correlates with overall levels of resource provisioning in the landscape and can be used to identify periods of low resource availability for bees (Couvillon et al. 2014). In the Amazon region, wet season months (November to April) are considered 'dearth periods' for stingless bees, as the number of food plants in their diet (e.g. pollen types), and food stores within colonies, decline significantly during this period relative to the dry season (May to October) (Marques-Souza et al. 1996; Veiga et al. 2013; Gomes et al. 2015). Therefore, the larger foraging distances reported during the rainy season could signify that *S.* aff. *postica* colonies actively expanded their foraging radius in periods of low resource availability, as found in honeybees and bumblebees (Westphal et al. 2006; Couvillon et al. 2014).

Broadly, these results suggest that *S.* aff. *postica* colonies are more stressed during the Amazonian wet season. Thus, any effort to provide additional floral resources, or supplement hives with artificial nectar and pollen foods, would be most beneficial during this period. Furthermore, as *Scaptotrigona* species are flower generalists (Marques-Souza et al. 2007; Aleixo et al. 2017), these results

are likely relevant for the conservation of other flower-visiting insects in the Amazon region. However, unlike honeybee 'waggle dances', results of translocation experiments can also be affected by external factors, including weather conditions and competition with other flower-visiting insects (Couvillon et al. 2014). Therefore, caution is required when attributing causality between shifts in floral resource availability and foraging distance without knowledge of intranidal communication mechanisms. Furthermore, changes in nectar sugar concentration alone did not explain temporal patterns in bee homing distance. As bee species use different plant species for nectar and pollen collection, seasonal changes in nectar plant availability may not necessarily correlate with flowering periods of key pollen plants (Aleixo et al. 2017), which may be a more important determinant of eusocial bee foraging activities. Further experiments using other species, across whole seasons, and which evaluate both collected and available floral resources from nearby habitats, would reduce the uncertainty associated with these hypotheses. Finally, the replication of homing experiments in multiple landscapes (e.g. degraded versus preserved landscapes) would allow investigation of how surrounding habitat structure also affects bee homing distances, for example, whether bees preferentially forage in natural habitats (e.g. forests) over human-modified areas (e.g. urban land, crop fields, pastures) (Leonhardt et al. 2016). Such an approach would minimise problems of non-independence between habitat types and the influence of potential confounding variables (e.g. prevailing winds, microclimates) on bee responses in single landscapes (Leonhardt et al. 2016).

In summary, our study provides a first insight into the temporal variation homing range of *S.* aff. *postica*, an economically important neotropical stingless bee species. Further research should test whether similar patterns exist in other neotropical stingless bee species, across multiple years and utilising different methodologies to ascertain greater degree of accuracy in determining actual foraging distances.

ACKNOWLEDGEMENTS

AUTHORS' CONTRIBUTION

AJC and FALC devised the experiment; AJC, RLCG, and KCS performed experiments; AJC analysed data and wrote initial draft; all authors contributed to subsequent drafts and approved the final manuscript.

FUNDING INFORMATION

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest The authors declare that they have no conflict of interest.

Variation temporelle de la capacité de repérage de l'abeille néotropicale *Scaptotrigona* aff. *postica* (Hymenoptera: Apidae: Meliponini).

distance de butinage / abeilles sans dard / forêt tropicale amazonienne / pollinisateurs tropicaux

Zeitliche Variation im Heimfindevermögen der neotropischen stachellosen Biene *Scaptotrigona* aff. *postica* (Hymenoptera: Apidae: Meliponini).

Sammelradius / stachellose Bienen /Amazonischer Regenwald / tropischer Regenwald

REFERENCES

Aleixo, K.P., Menezes, C., Imperatriz Fonseca, V.L. & da Silva, C.I. (2017) Seasonal availability of floral resources and ambient temperature shape stingless bee foraging behavior (*Scaptotrigona* aff. *depilis*). Apidologie. **48**, 117–127.

Araújo, E.D., Costa, M., Chaud-Netto, J. & Fowler, H.G. (2004) Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. Braz. J. Biol. **64**, 563–568.

Archer, C.R., Pirk, C.W.W., Carvalheiro, L.G. & Nicolson, S.W. (2014) Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. Oikos. **123**, 401–407.

Ballantyne, G., Baldock, K.C.R., Rendell, L. & Willmer, P.G. (2017) Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. Sci. Rep. **7**, 8389.

Barton, K. (2015) MuMIn: Multi-model inference. R package version 1.9.13. Version, 1, 18.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**, 1–48.

Bawa, K.S. (1990) Plant-pollinator interactions in tropical rain forests. Annu. Rev. Ecol. Syst. **21**.

Brown, J.C. & De Oliveira, M.L. (2014) The impact of agricultural colonization and deforestation on stingless bee (Apidae: Meliponini) composition and richness in Rondônia, Brazil. *Apidologie*. **45**, 172–188.

Camargo, J.M.F. & Pedro, S.R.M. (2013). Meliponini Lepeletier, 1836. In Moure, J.S., Urban, D. & Melo, G.A.R. (Orgs). Catalogue of Bees (Hymenoptera. Apoidea) in the Neotropical Region [online] http://www.moure.cria.org.br/catalogue. Accessed 3 July 2019.

Cane, J.H. (1987) Estimation of Bee Size Using Intertegular Span (Apoidea). J. Kansas Entomol. Soc. **60**, 145–147.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. Theor. Popul. Biol. **9**, 129–136.

Cortopassi-Laurino, M., Imperatriz-Fonseca, V.L., Roubik, D.W., Dollin, A., Heard, T., Aguilar, I., Venturieri, G., Eardley, C. & Nogueira-Neto, P. (2006) Global meliponiculture: challenges and opportunities. Apidologie. **37**, 275–292.

Couvillon, M.J., Schürch, R. & Ratnieks, F.L.W. (2014) Waggle Dance Distances as Integrative Indicators of Seasonal Foraging Challenges. PLoS One. **9**, e93495.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. J. Anim. Ecol. **71**, 757–764.

Giannini, T.C., Boff, S., Cordeiro, G.D., Cartolano Jr., E.A., Veiga, A.K., Imperatriz-Fonseca, V.L. & Saraiva, A.M. (2015) Crop pollinators in Brazil: a review of reported interactions. Apidologie. **46**, 209–223.

Gomes, R.L.C., Menezes, C. & Contrera, F.A.L. (2015) Worker longevity in an Amazonian *Melipona* (Apidae, Meliponini) species: effects of season and age at foraging onset. Apidologie.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. Oecologia. **153**, 589–596.

Hrncir, M. & Maia-Silva, C. (2013) On the Diversity of Foraging-Related Traits in Stingless Bees, in: Vit, P., Pedro, S.R.M., & Roubik, D. (eds), Pot-Honey: A legacy of stingless bees. Springer New York, New York, NY, pp. 201–215

Instituto Nacional de Meteorologia - INMET (2019) [online] http://www.inmet.gov.br/portal/ (accessed on 03 July 2019).

Jaffé, R., Pope, N., Carvalho, A.T., Maia, U.M., Blochtein, B., de Carvalho, C.A.L., Carvalho-Zilse, G.A., Freitas, B.M., Menezes, C., de Fátima Ribeiro, M., Venturieri, G.C. & Imperatriz-Fonseca, V.L. (2015) Bees for Development: Brazilian Survey Reveals How to Optimize Stingless Beekeeping. PLoS One. **10**, e0121157.

Jarau, S. (2009) Chemical communication during food exploitation instingless bees, in: Jarau, S. & Hrncir, M. (eds), Food Exploitation bysocial insects: ecological, behavioral, and theoretical approaches. CRC University Press, Taylor and Francis Group Boca Raton, pp. 233–244

Kerr, W.E., Ferreira, A. & de Mattos, N.S. (1963) Communication among Stingless Bees-Additional Data (Hymenoptera: Apidae). J. New York Entomol. Soc. **71**, 80–90.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. R. Soc. **274**, 303–313.

Kuhn-Neto, B., Contrera, F.A.L., Castro, M.S., Nieh, J.C., Silva, A.G., Pinto, R.S., Contrera, F.A.L., Albuquerque, P.M.C. & Rêgo, M.M.C. (2009) Long distance foraging and recruitment by a stingless bee, *Melipona mandacaia*. Apidologie. **40**, 472–480.

Leão, K.L., Queiroz, A.C.M., Veiga, J.C., Contrera, F.A.L., & Venturieri, G.C. (2016) Colony Development and Management of the Stingless Bee Scaptotrigona aff. postica (Apidae: Meliponini) Using Different Hive Models. Sociobiology. **63**, 1038–1045.

Leonhardt, S.D. (2017) Chemical Ecology of Stingless Bees. J. Chem. Ecol. **43**, 385–402.

Leonhardt, S.D., Kaluza, B.F., Wallace, H. & Heard, T.A. (2016) Resources or landmarks: which factors drive homing success in *Tetragonula carbonaria* foraging in natural and disturbed landscapes? J. Comp. Physiol. A:

Neuroethol. Sens. Neural Behav. Physiol. **202**, 701–708.

Marques-Souza, A.C., De Oliveira Moura, C. & Nelson, B.W. (1996) Pollen collected by *Trigona williana* (Hymenoptera: Apidae) in Central Amazonia. Rev. Biol. Trop. **44**, 567–573.

Marques-Souza, A.C., Absy, M.L. & Kerr, W.E. (2007) Pollen harvest features of the Central Amazonian bee *Scaptotrigona fulvicutis* Moure 1964 (Apidae: Meliponinae), in Brazil . Acta Bot. Bras. **21**, 11–20.

Michener, C. (2007) The Bees of the World, 2nd edition. Johns Hopkins University Press. Baltimore and London.

Nieh, J.C. (2004) Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). Apidologie. **35**, 159–182.

Pahl, M., Zhu, H., Tautz, J. & Zhang, S. (2011) Large scale homing in honeybees. PLoS One. **6**.

Pasquet, R.S., Peltier, A., Hufford, M.B., Oudin, E., Saulnier, J., Paul, L., Knudsen, J.T., Herren, H.R. & Gepts, P. (2008) Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. Proc. Natl. Acad. Sci. **105**, 13456–13461.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. **11**, 1633–1644.

Pedro, S.R.M. (2014) The Stingless Bee Fauna In Brazil (Hymenoptera: Apidae). Sociobiology. **61**, 348–354.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2016) nlme: Linear and Nonlinear Mixed Effects Models. *R package version*, R package, 1–86

R Core Team (2017) R. R Core Team

Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., et al. (2016) Non-bee insects are important contributors to global crop pollination. Proc. Natl. Acad. Sci. **113**, 146–151.

Roubik, D.W. & Aluja, M. (1983) Flight Ranges of *Melipona* and *Trigona* in Tropical Forest. J. Kansas Entomol. Soc. **56**, 217–222.

Silva, A.G., Pinto, R.S., Contrera, F.A.L., Albuquerque, P.M.C. & Rêgo, M.M.C. (2014) Foraging distance of *Melipona subnitida* Ducke (Hymenoptera: Apidae). Sociobiology. **61**, 494–501.

Slaa, E.J., Chaves, L.A.S., Malagodi-Braga, K.S. & Hofstede, F.E. (2006) Stingless bees in applied pollination: practice and perspectives. Apidologie. **37**, 293–315.

Smith, J.P., Heard, T.A., Beekman, M. & Gloag, R. (2017) Flight range of the Australian stingless bee *Tetragonula carbonaria* (Hymenoptera: Apidae). Austral Entomol. **56**, 50–53.

Steffan-Dewenter, I. & Kuhn, A. (2003) Honeybee foraging in differentially structured landscapes. Proc. R. Soc. B: Biol. Sci. **270**, 569–575.

van Nieuwstadt, G.L.M. & Ruano Iraheta, E.C. (1996) Relation between size and foraging range in stingless bees (Apidae, Meliponinae). Apidologie. **27**, 219–228.

Vanbergen, A.J. (2013) Threats to an ecosystem service: Pressures on pollinators. Front. Ecol. Environ. **11**, 251–259.

Veiga, J.C., Menezes, C., Venturieri, G.C. & Contrera, F.A.L. (2013) The bigger, the smaller: relationship between body size and food stores in the stingless bee *Melipona flavolineata*. Apidologie **44**, 324–333.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2006) Foraging trip duration of bumblebees in relation to landscape-wide resource availability. Ecol. Entomol. **31**, 389–394.

Wiens, J.A., Stenseth, N.C., Van Horne, B. & Ims, R.A. (1993) Ecological Mechanisms and Landscape Ecology. Oikos. **66**, 369–380.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. **143**, 669–676.

Publisher's note   Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.