

RESEARCH ARTICLE

Getting older, getting smarter: ontogeny of foraging behaviour in the tropical social wasp *Ropalidia marginata*

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ABSTRACT

Desert ants and honey bees start foraging when they are a few days old, and subsequently increase their foraging effort and the amount of foraged food. This could be an optimal strategy for scavenger/gatherer animals inhabiting landscapes with fewer features. However, animals inhabiting cluttered landscapes, especially predatory animals, may require substantial familiarity with foraging landscapes to forage efficiently. They may acquire such spatial familiarity with increasing age/experience, and eventually reduce their foraging effort without compromising on foraging success/efficiency. To check whether this holds for the individually foraging predatory tropical paper-wasp *Ropalidia marginata*, we recorded the number and duration of all foraging trips, the identity of foraged materials, and the directions of outbound and inbound flights (with respect to the nest) of known-age wasps for three consecutive days from three naturally occurring colonies; thus, we measured behavioural profiles of wasps of various ages, and not from the same wasp throughout its lifespan. Wasps increased their foraging duration rapidly until about 4 weeks of age, during which they rarely brought food, although some wasps brought building material and water. Thereafter, their foraging duration started decreasing. Nevertheless, their foraging success/efficiency in bringing food kept on increasing. With age, wasps developed individual directional preferences for outbound and inbound flights, indicating the development of spatial memory for rewarding sites. Also, the angular difference between their outbound and subsequent inbound flights gradually increased, indicating older wasps may have followed tortuous foraging routes. High investment in early life to acquire familiarity with foraging landscapes and using that later to perform efficient foraging could be an optimal strategy for individually foraging animals inhabiting feature-rich landscapes.

KEY WORDS: Foraging strategy, Spatial learning and memory, Social hymenoptera, Evolution, Behavioural ecology

INTRODUCTION

Minimising foraging effort without compromising foraging gain is a perpetual challenge for foraging animals. Learning and memorising features of foraging landscapes, especially those related to the location of rewards, could be an efficient strategy for animals to collect substantial foraged materials with minimal foraging effort (Caraco, 1980; Kamil and Roitblat, 1985). It has been postulated that

spatial familiarity increases with the time an animal travels within a landscape (Boyer and Walsh, 2010), which, in turn, enables animals to attain greater foraging benefits (Bracis et al., 2015; Dukas and Visscher, 1994; Pyke et al., 1977; Raine and Chittka, 2008). However, foraging is a costly affair in terms of time, energy and associated risks such as predation. Thus, it would be a proficient strategy for animals to strike an optimum balance between their foraging gains and the time they invest to attain familiarity with their foraging landscapes and in foraging (Abrams, 1991; Norberg, 1977).

Foragers of social hymenopterans such as ants (Fleischmann et al., 2016), honey bees (Capaldi et al., 2000; Degen et al., 2015) and bumble bees (Osborne et al., 2013; Woodgate et al., 2016) begin their foraging life with a few exploratory walks/flights, through which they establish spatial coordination with their nest and the surrounding landscape, and start foraging for food on the same day. Sahara Desert ants scavenge for sparsely distributed animal carcasses in featureless desert landscapes; they increase their foraging duration and their foraging success with the advancement of their short foraging life (Wehner et al., 2004). Similarly, the honey bee, a gatherer that evolved in temperate landscapes, also increases foraging gain with age by covering a greater foraging area per trip and increasing flight speed (Capaldi et al., 2000). Thus, foraging success in desert ants and honey bees seems to depend much on their current foraging effort, and not on the effort invested in the exploratory/learning phase. This might be an ideal strategy for foragers that evolved in landscapes with a lower density of features. In contrast, landscapes with a high density of features, as in the tropics, offer significantly more spatial information but less visual continuity (Cartwright and Collett, 1987; Zeil, 2012). Thus, insects inhabiting complex feature-rich terrains encounter homing challenges different from those of insects inhabiting feature-poor terrains, and they may therefore evolve with different homing and foraging strategies. Interestingly, insects inhabiting feature-poor landscapes, like the desert ants, rely heavily on their path integration system for homing. In contrast, foragers of the Australian ant *Melophorus bagoti* (Cheng et al., 2014; Narendra, 2007; Wystrach et al., 2011) inhabiting semi-desert cluttered landscape and the tropical ant *Gigantiops destructor* (Macquart et al., 2006) inhabiting complex tropical rainforests rely heavily on learnt visual features of their foraging landscape. However, we are yet to know the strategies by which social insects that evolved in feature-rich landscapes develop their foraging abilities. We hypothesize that compared with insects that evolved in feature-poor landscapes, these insects may need to invest more time before they start foraging for food. They may obtain the required spatial familiarity with their foraging landscapes in their initial foraging phase; this may eventually enable them to visit rewarding sites with much less or even no large-scale searching (i.e. searching throughout the landscape), and thus increase their foraging gain while reducing foraging effort.

Ropalidia marginata is an aseasonal predatory social wasp inhabiting feature-rich tropical landscapes of peninsular India.

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Females typically survive for 9–329 days (mean±s.d. 135.9±86.3 days) in laboratory conditions (Sen and Gadagkar, 2010) and colonies typically consist of 1–200 females (mean±s.d. 21.9±22.3) (Gadagkar, 2001). Young wasps begin their working life with intranidal tasks; as they advance in age, they gradually increase the proportion of extranidal tasks (i.e. foraging) (Naug and Gadagkar, 1998). These wasps forage solitarily for food (spiders, larvae of other insects, etc.), building materials (plant fibres) and water. Foragers often cut large prey items into pieces and bring those pieces to their nest in multiple bouts. These wasps typically forage within about 500 m of their nests (Mandal and Gadagkar, 2015) and experienced foragers possess comprehensive spatial familiarity with their foraging landscapes (Mandal et al., 2017). As these wasps forage solitarily, each forager has to acquire this spatial familiarity. Thus, *R. marginata*, being a predatory, solitary foraging, long-lived, tropical flying insect, is markedly different from honey bees (nectar- and pollen-gathering flying insects with a much shorter lifespan that recruit nestmates to food-collecting sites, and that evolved in a temperate landscape) and desert ants (walking scavengers also with a shorter lifespan that evolved in the desert landscape), two other closely related and well-studied social insects.

Here, we asked whether *R. marginata* has evolved foraging strategies different from those of honey bees and desert ants. In particular, we tested whether foragers of *R. marginata* spend a substantial amount of time outside their nest during the initial phase of their foraging life (probably for exploring and learning the features of the foraging landscape), and subsequently reduce foraging effort without affecting foraging success/efficiency. We also predicted that individual foraging wasps attain foraging competence by developing sector fidelity for foraging [i.e. fidelity to go towards a particular (rewarding) direction for foraging], as ants (Wehner et al., 2004) and bees (Capaldi et al., 2000) are known to do. Young wasps may not develop such a choice for any particular direction during their exploratory phase until they encounter a rewarding patch (for instance, a food source). We tested this prediction by analysing all the outbound flight directions of individual wasps.

While insects rely highly on the proprioception and internal/external compass-based path integration system during early foraging bouts, they shift their reliance to learnt spatial information with the advancement of age/experience (Bühlmann et al., 2011; Cheng et al., 2012; Kohler and Wehner, 2005; Menzel and Greggers, 2015; Müller and Wehner, 2010; Narendra, 2007; Wystrach et al., 2014). As path integration is an error-prone system and the error increases with directional changes during a trip (Heinze et al., 2018), young and inexperienced foragers are expected to go out and return along the same path for a particular trip, though they may choose different directions for subsequent trips (Capaldi et al., 2000). However, familiarity with the landscape may gradually enable foragers to develop a preference for habitual foraging directions (Osborne et al., 2013; Woodgate et al., 2016) and novel foraging routes (Menzel et al., 1998). Such spatial familiarity may eventually enable them to sequentially explore several places in different directions during a single trip (Hassell and Southwood, 1978) by developing multi-destination ‘trapline’ routes (Buatois and Lihoreau, 2016; Lihoreau et al., 2012; Saleh and Chittka, 2007), and consequently to attain higher foraging gain with reduced foraging effort. Therefore, after each foraging bout, experienced foragers may return from the direction of the site of their last visit. Here, we also tested whether wasps developed any directional preference for their inbound flights and whether the angular difference between the outbound and subsequent inbound directions increased with advancing age.

MATERIALS AND METHODS

Although collecting data from individual wasps throughout their lifespan would have been ideal for answering the questions we were interested in, executing such an approach in the field with a sufficient sample size is not feasible, especially for such a long-lived animal. Therefore, we used a proxy method: we collected data for three consecutive days on all the foraging trips made by all forager wasps of all ages from three naturally occurring nests (N17, N18 and N21) of *Ropalidia marginata* (le Peletier 1836) (Vespidae, Polistinae). All three nests were located at the Indian Institute of Science campus, Bangalore, India (13°01'N, 077°34'E). The main campus is spread over an area of about 1.55 km² and the landscape is dominated by densely distributed trees (with an average height of about 30 m) and shrubs covering about 75% of the landscape, along with small to medium-sized (i.e. maximum height of about 35 m) academic and residential buildings, limiting a continuous view to a maximum distance of ~30 m on the ground (Fig. S1). An uninterrupted view for a longer distance could only be obtained on campus roads of various lengths with a width of 3–6 m, and with light motor traffic. Such a landscape is of special interest, as foraging wasps typically cruise within a height of 2–10 m from the ground and thus can access a very small visual catchment area during their regular foraging trips.

We found all three experimental nests inside electrical fuse boxes attached to roadside lampposts at a height of about 50 cm from the ground. Immediately after locating the nests, we sealed all the holes on the boxes except the one on the front lid to allow the wasps to become accustomed to this being the only exit and entrance. We also placed a mimic of the video camera 30 cm away from the front lid of the boxes to allow the foraging wasps to get used to it, and this remained in position until we replaced it with the real video camera for data collection (Fig. S2). We took necessary precautions while working close to the electrical fuse boxes. We carried out the experiment in three consecutive steps, as detailed below.

Step 1: accounting for the age of the wasps

As the first step of our experiment, we needed to know the age of the wasps. After locating each nest, we conducted a daily census of the wasp colonies at night using a headlamp emitting low-intensity red light. Whenever we found a newly enclosed wasp, we uniquely colour-marked it on its thorax and/or abdomen with Testors[®] quick-dry enamel paints and recorded its date of eclosion. To colour-mark the wasps, we gently applied the paint to the stationary wasps on the nest using the tip of a 15 cm long matchstick. We continued to do this until we attained the age of all the resident wasps of the colony. We conducted the daily census for 120, 161 and 105 days for nests N17, N18 and N21 (starting on 1 October, 11 November and 23 December 2013), respectively, before we began collecting data.

Step 2: data collection

Next, we replaced the dummy camera with a real motion-sensitive web camera (Logitech HD Pro C920) and connected that to a laptop kept at least 5 m away from the lampposts. The camera was set to start recording (with 2 s of pre-recording function, using Webcam Zone Trigger[™] software) upon detection of any movement within its field of view (which included the hole on the front lid of the box and part of the front lid, see Fig. S3). Thus, the video captured the identity of all the outbound/inbound wasps when they appeared within the camera's field of view, the time of their departure/arrival and the identity of foraged materials, if any. An observer sat near the laptop in camouflage attire, and audio-recorded data on the vanishing bearing (synced with the video data) of the outbound

and inbound flights performed by the wasps (along with deterring curious birds, squirrels and monkeys from disrupting the set-up). From such a distance, the observer could see the flight direction of the wasps but not the colour marks on them; hence, the observer was blind to the identity of the foragers during data collection. Later, we identified the wasps and corresponding vanishing bearings through the audio-synced video. We included the vanishing bearings of the outbound wasps in the analysis only if the wasps could be followed for at least 5 m. Similarly, for the inbound wasps, we included data in the analysis only when the observer first noticed the wasp when it was at least 5 m away from its nest. We recorded the direction of the outbound and inbound flights in 10 deg intervals (marked by transects) in which the vanishing bearings fell (keeping the nest in the centre, and scoring 0, 90, 180 and 270 deg for geomagnetic north, west, south and east, respectively, for instance). To become adept with the transects and to obtain accurate data on the vanishing bearings, for each nest we performed the whole experiment for at least one full day before collecting the data we used for the analyses. For each nest, we collected data for three consecutive days. Each day, we turned on the set-up for video recording at least 5 min before sunrise and stopped it after sunset. Thus, we conducted observations for a total of 30 h 45 min (10 h 15 min per day) for N17 on 29, 30 and 31 January 2014, 38 h 15 min (12 h 45 min per day) for N18 on 21, 22 and 23 April 2014 and 37 h 30 min (12 h 30 min per day) for N21 on 7, 8 and 9 April 2014. The data consisted of 78, 89 and 105 unique foraging wasps from N17, N18 and N21, respectively.

Step 3: data analysis

We performed all statistical analyses using RStudio interface 0.99.891 for R version 3.2.2. For each wasp, we calculated the number of foraging trips, the proportion of time spent outside the nest, average trip duration, foraging performance (as foraging success and foraging efficiency; see below for definition), consistency in the direction of outbound and inbound trips, and, for each trip, the angular difference between the direction of outbound flight and subsequent inbound flight. Then, we checked for potential relationships between these parameters and the age of the wasps (in days).

We defined the proportion of time spent outside the nest as the ratio of the total time that a wasp spent outside its nest during the 3 days of observation to the total observation time for that nest. To determine patterns in the relationships between the proportion of time wasps spent outside their nest and their age, we fitted three mathematical functions to the data separately for each of the three nests: a linear and a quadratic function with an assumption of symmetry of the data, and an asymmetric non-linear rational function, namely Holling type IV, which has a characteristic rapid initial increase followed by a gradual decrease (Bolker, 2008). The Holling type IV function was fitted to the data with non-linear least squares regression and was expressed as $(A \times \text{age}^2)/(B + C \times \text{age} + \text{age}^2)$, where A is the proportion of time spent outside when the curve approaches its asymptote, and $-2 \times B/C$ demarcates the age at the peak of the curve. Similarly, we calculated the average duration of foraging trips by dividing the total time a wasp spent on foraging in 3 days by the total number of trips it had made in the 3 days and determined the best fitting relationship with the age of the wasps.

We computed foraging success as the ratio of the number of trips in which a wasp brought food to its nest to the total number of trips it made. We computed foraging efficiency as the number of times the wasp brought food to the nest divided by the proportion of time it spent outside of its nest. For each nest, we fitted a linear and a

quadratic function to explore the relationships between both foraging success and foraging efficiency and the age of the wasps.

Next, we examined whether, with age, wasps developed a preference for any particular direction when going out to forage. We calculated their directional preference by measuring the length of the mean vector (r -value) (Batschelet, 1981) of all the outbound directions taken by each wasp on a day, and averaging the data collected over 3 days. We eliminated those wasps from our analysis for which we had data for only one outbound trip in a day. Thus, our dataset for this analysis comprised 54 (for N17), 71 (for N18) and 68 (for N21) unique wasps. We fitted a linear and a saturating function, namely Michaelis–Menten, to the data, and calculated which function explained the data better. The expression of the Michaelis–Menten function was $(A \times \text{age})/(B + \text{age})$, where A defines the value of the dependent variable (r -value) at the asymptote and B defines the value of the independent variable (age of wasps) at $A/2$. Similarly, we measured whether, with age, wasps developed any directionality for their inbound trips. Here, the dataset comprised 51, 71 and 80 unique wasps from N17, N18 and N21, respectively. As we wanted to verify whether, after an initial increase, wasps reduced the directionality of their inbound trips, we fitted a quadratic function along with the linear and Michaelis–Menten function to the data and determined the best fit.

To verify whether the wasps started taking detours with increasing age, we calculated the angular difference between the direction of the outbound and subsequent inbound flights for each trip of each wasp. The angular difference ranged from 0 to 180 deg. Although extrapolating the entire foraging route from the outbound/inbound directional data acquired only from a distance of 5 m around their nests could amount to over-speculation, our data provide a rough estimate of the foraging route during a trip, assuming a greater angular difference indicates a greater detour during their foraging trip. The dataset comprised 403, 698, 783 data points from 51, 71 and 80 unique wasps from N17, N18 and N21, respectively; we fitted a generalised linear mixed-effects model (using the lme4 package) with a Poisson error family and log link, using data from all the wasps from all three nests together. We took the rescaled value (not the transformed value; this results in better explanatory power of the model) of the angular difference between the outbound and inbound direction as the response variable (using the ‘scales’ package in R; <https://CRAN.R-project.org/package=scales>), the age of the wasps as the explanatory variable, and the identity of the wasps nested within their colony ID as random effects.

RESULTS

Characteristics of foragers

During the 3 days of observation, 78, 89 and 105 unique wasps from nests N17, N18 and N21 made a total of 607, 1173 and 2407 foraging trips, respectively. On the basis of the material that a wasp brought back to its nest, most of the wasps (100%, 95.5% and 92.37% from N17, N18 and N21, respectively) could be classified into four categories: wasps that did not bring anything back, and those that brought building material, water or food to their nests. However, there were a few cases in which a single wasp brought more than one material (see Table S1). We found that the water foragers (defined as wasps that brought water more than once and more than anything else; 2, 1 and 8 wasps in N17, N18 and N21, respectively) made a much greater number of trips than other foragers; in fact, all water foragers were outliers based on the total number of trips they took. Compared with foragers that brought other things, trip duration of the water foragers was significantly shorter (GLMM, estimate=0.765, z -value=141.72, $P < 0.01$) and

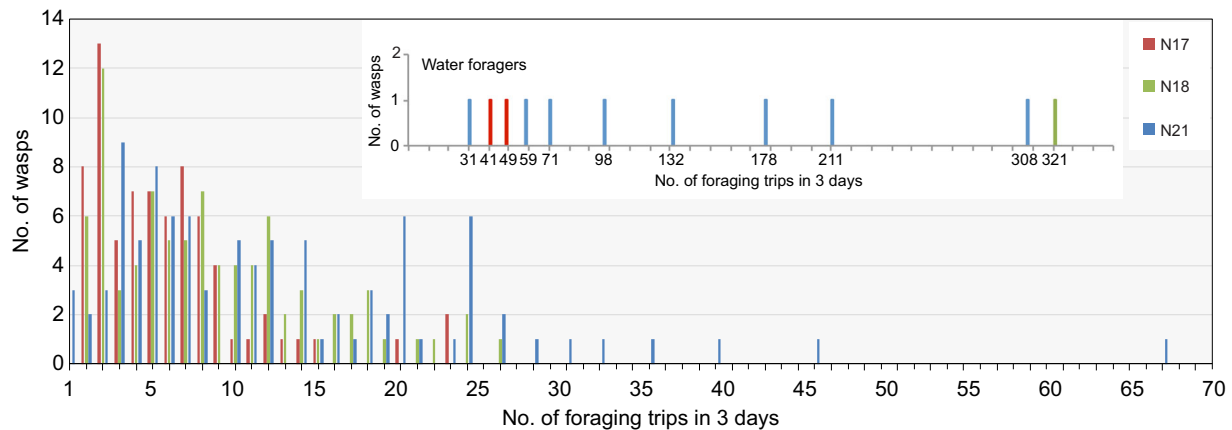


Fig. 1. Number of foraging trips performed by *Ropalidia marginata* wasps from three nests (N17, N18 and N21) during the 3 days of observation. The number of trips made by the water foragers was much greater than that by the other foragers (see Table S1), and inclusion in this graph would have made visualisation of data from the other wasps difficult. Therefore, data for the water foragers are presented in the inset.

they had a significantly higher success rate (χ^2 -test, $P < 0.01$ for all three nests, $\chi^2 = 14.03$ for N17, 278.07 for N18, 259.3 for N21) (Table S1). They showed high directionality for outbound as well as inbound trips (r -value on any given day was greater than 0.9 for all water foragers), and had much less angular difference between outbound trips and the subsequent inbound trip than the other foragers (GLMM, estimate = 0.3545, z -value = 10.60, $P < 0.01$). For these reasons, we excluded water foragers from all the analyses except those that we performed to ascertain the relationships between wasp age and foraging duration. For an overview of the foraging activities on these three nests, see Fig. 1 and Table S1.

We found that the wasps which brought food at least once to their nest were among the oldest in their colony (linear mixed-effect model, estimate = 32.95, s.e. = 1.94, $t = 17.00$, $P < 0.01$; Fig. S4), and the wasps that did not bring anything to their nest were amongst the youngest (estimate = 27.62, s.e. = 2.28, $t = 12.11$, $P < 0.01$). As the number of wasps that brought building materials and water was much lower than the number that brought food or did not bring anything, we performed a Mann–Whitney U -test with Monte Carlo permutation with 10,000 iterations to check for any pattern between

the age of the wasps and what they brought to their nests. We found that the water foragers were significantly younger than the foragers that brought food in all three nests ($P < 0.01$ for all three nests), and wasps that brought building materials were significantly younger than the water foragers in N17 and N21 ($P < 0.02$; for N18, $P = 0.94$). However, we could not detect any significant difference between the age of the foragers that did not bring anything and those that brought building materials ($P = 0.22$, 0.12 and 0.17 for N17, N18 and N21, respectively) (see Fig. S5A–C).

Change in the number of foraging trips per day with age

Wasps from all three nests initially increased and later decreased the number of foraging trips per day with increasing age. A quadratic function explained the rate of change better than a linear function (ANOVA, $P < 0.05$ for all three nests, $F = 14.46$, 9.44 and 8.07 for N17, N18 and N21, respectively) (Fig. 2).

Change in the proportion of time spent foraging with age

A linear fit explained only 14.91% (AIC = -64.09), 18.28% (AIC = -8.44) and 26% (AIC = -16.92) of the total variation of

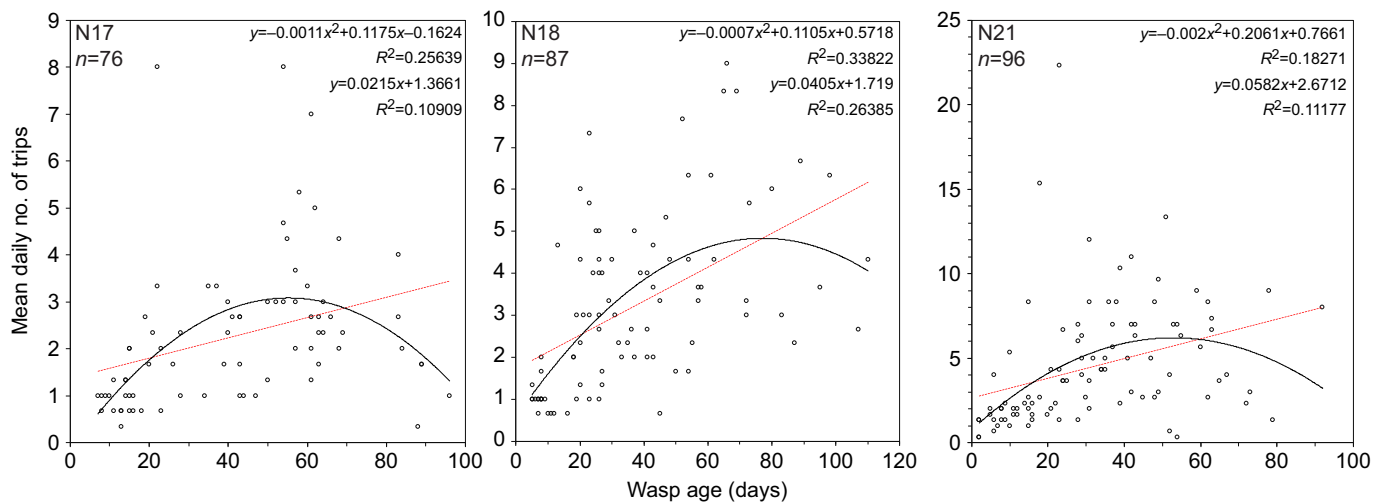
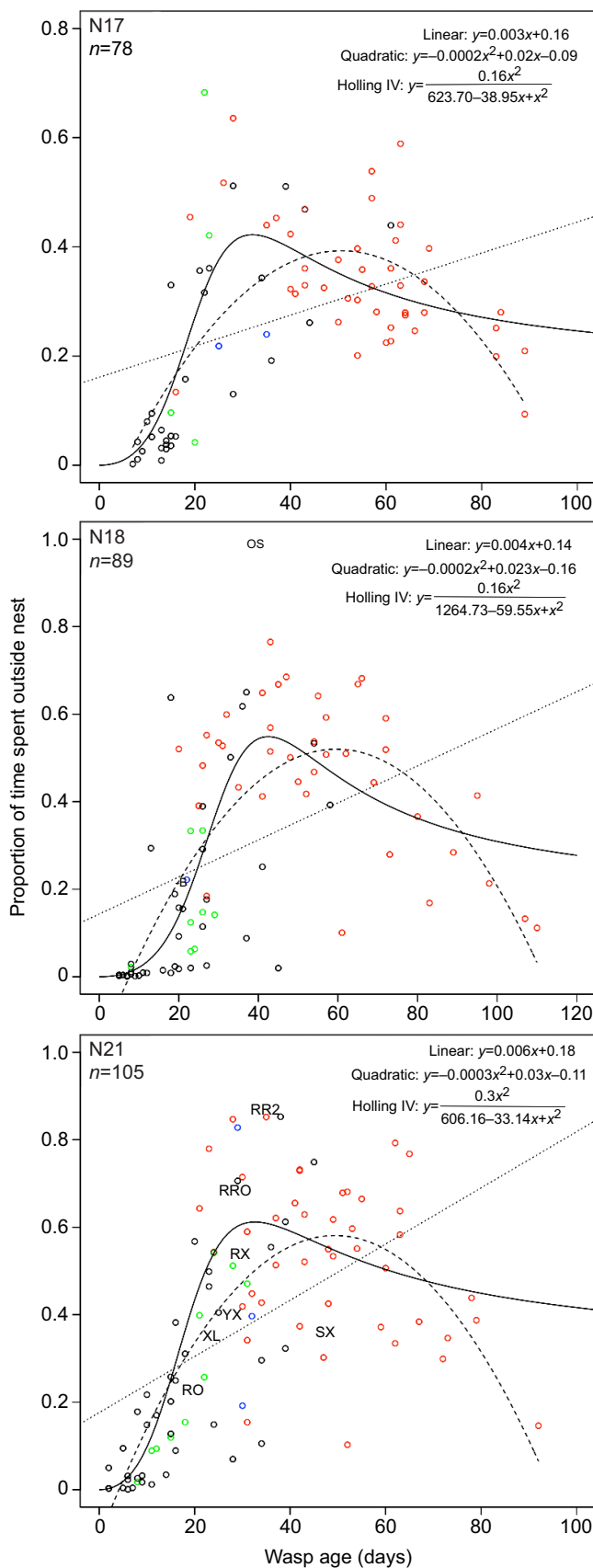


Fig. 2. Change in the daily number of foraging trips with age. For all three nests, a quadratic model (black line) explained more variation of the data than a linear model (red line). Comparison of AIC values of the linear (AIC = 282.36 for N17, AIC = 348.82 for N18, AIC = 512.95 for N21) and quadratic model (AIC = 270.63 for N17, AIC = 341.56 for N18, AIC = 506.96 for N21) reconfirmed the better fit of the quadratic model (ANOVA, $P < 0.05$). An attempt to fit a Holling type IV function revealed non-significant values of the parameters for all three nests. Note, we did not include water foragers in this analysis.



the relationship between the age of the wasps and the proportion of time they spent outside their nest for N17, N18 and N21, respectively. The quadratic model explained 46.29% (AIC=−98.98), 53.10%

Fig. 3. Change in the proportion of time wasps spent on foraging with age. Foraging time was measured as the time spent outside the nest. In the plots, black circles represent wasps that did not bring anything to their nest during the 3 days of observation. Green, blue and red circles represent wasps that brought building material, water and food, respectively, at least once to their nest. One wasp (−B) in N18 and three wasps (RO, XL, YX) in N21 brought both building material and water; one wasp (OS) in N18 brought both water and food; three wasps (RR2, RRO, RX) from N21 brought building material and food; one wasp (SX) from N21 brought building material, water and food. Three mathematical functions (linear, dotted line; quadratic, dashed line; and Holling type IV, solid line) were fitted to the data from each nest. For all three nests, Holling type IV provided the best fit. For all the parameters of this function, $P<0.05$ for all nests.

(AIC=−55.86) and 55.31% (AIC=−67.87) of the total variation of the data from N17, N18 and N21, respectively. When we fitted the Holling type IV function to the data, a greater amount of variation in the data was explained with decreased AIC values (N17: 54.46%, AIC=−111.85; N18: 54.74%, AIC=−59.02; N21: 55.98%, AIC=−69.45) (Fig. 3). It is noteworthy that the few young individuals that brought food (red circles in Fig. 3) generally spent a greater amount of time outside of their nest while the older wasps that brought food spent a varied amount of time outside their nest.

Change in average foraging duration per trip with age

Similarly, we explored patterns between age and the average foraging duration per trip of the wasps by fitting a linear, quadratic and Holling type IV function to the dataset. Here also, Holling type IV provided the best fit to the data from all three nests; it explained 31.45% (AIC=857.68) of the variation of the data [compared with 0.124% (AIC=885.04) by linear and 14.51% (AIC=874.90) by quadratic function] from N17, 41.49% (AIC=973.52) of the variation of the data [compared with 5.03% (AIC=1014.62) by linear and 32.4% (AIC=986.36) by quadratic function] from N18 and 15.45% (AIC=1164.27) of the variation of the data [compared with 4.08% (AIC=1175.52) by linear and 11% (AIC=1169.66) by quadratic function] from N21 (Fig. 4).

Change in foraging success with age

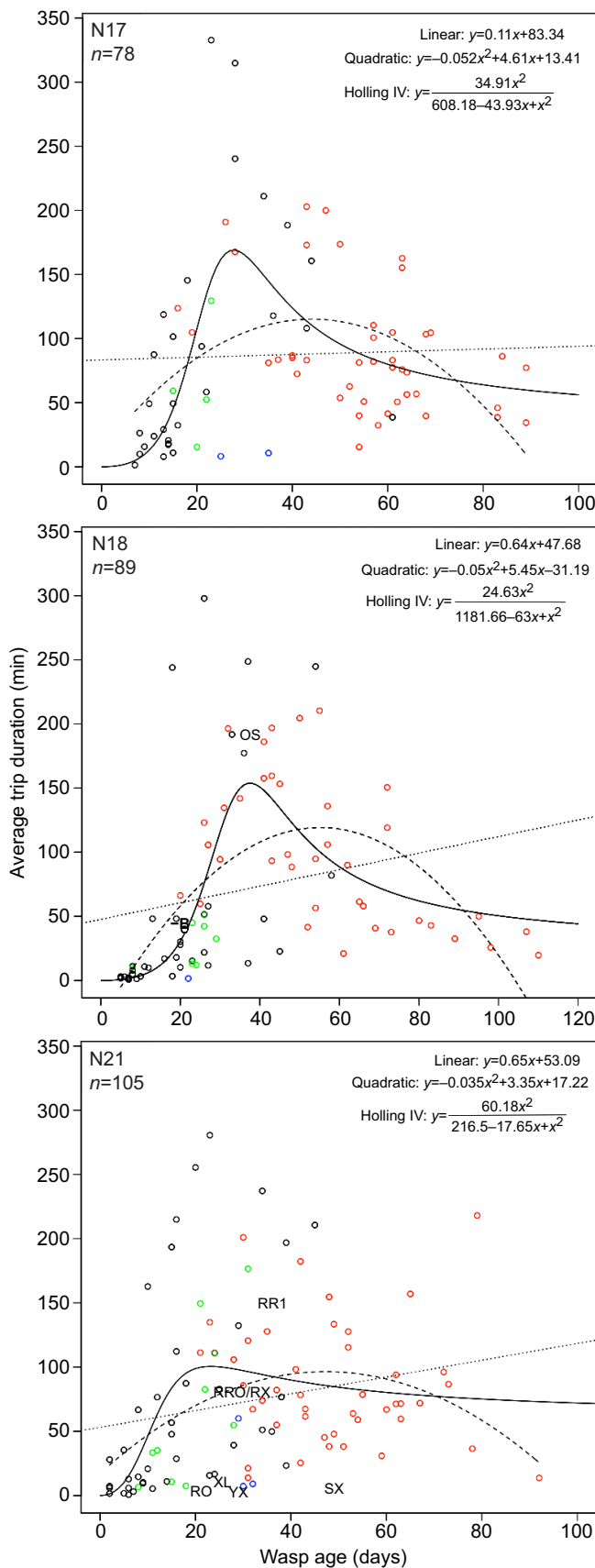
Foraging success of the wasps (i.e. the proportion of trips in which wasps brought food) from all three nests increased significantly with age ($P<0.05$) (Fig. 5). A linear model explained 57.17%, 47.73% and 40.95% of the variation of the data from N17, N18 and N21, respectively. Attempts to fit a quadratic function to the data revealed insignificant P -values (i.e. $P>0.05$) for all the parameters for N17 and N21, and a significant P -value ($P=0.027$) for the quadratic term for N18.

Change in foraging efficiency with age

Likewise, foraging efficiency (i.e. the number of times a wasp brought food to its nest per unit time it spent on foraging) also increased with the advancement of their age (Fig. 6). While all the parameters of linear models for all the nests were significant ($P<0.05$) (and explained 61.08%, 65.5% and 63% of the variation of the data from N17, N18 and N21, respectively), none of the parameters in the quadratic model were significant for N17, and only the quadratic term was significant for N18 and N21.

Developing directional fidelity for outbound trips with age

The average of mean vector length (r -value) of the outbound flight directions increased with the age of the wasps from all three nests. We found that the Michaelis–Menten function (Fig. 7) explained the data better than the linear function for all three nests. While the



former function explained 40.67%, 51.30% and 54.58% of the total variation of the data from N17, N18 and N21, respectively (AIC: -9.17 for N17, -26.66 for N18 and -48.01 for N21), the latter

Fig. 4. Change in average foraging duration with age. Average foraging duration per trip was also explained best by a Holling type IV function (solid line), which is characterised by a rapid initial ascent and, after reaching a peak, a gradual descent. For all the parameters of this function, $P<0.05$ for all the nests. As in Fig. 3, black, green, blue and red circles represent wasps that did not bring anything, and wasps that brought building material, water and food, respectively, at least once to their nest during the 3 days of observation. Similarly, one wasp (–B) in N18 and three wasps (RO, XL, YX) in N21 brought both building material and water; one wasp (OS) in N18 brought both water and food; three wasps (RR2, RRO, RX) from N21 brought building material and food; one wasp (SX) from N21 brought building material, water and food.

explained only 22.9%, 42.55% and 54.74% of the total variation in the data from N17, N18 and N21, respectively (AIC: 4.98 for N17, -15.95 for N18, -33.81 for N21).

Developing directional fidelity for inbound trips with age

Interestingly, the average of the mean vector length (r -value) of the inbound flights made by the wasps also increased with age. Whereas the Michaelis–Menten function best explained the data from N17 and N18, a quadratic function best explained the data from N21 (Fig. 8). While the linear function explained 16.92% (AIC= -14.44), 16.64% (AIC= -18.72) and 13.91% (AIC= -18.48) of the variation of the data from N17, N18 and N21, respectively, a quadratic function explained 24.6% (AIC= -17.38), 30.91% (AIC= -30.05) and 43.19% (AIC= -49.73), and the Michaelis–Menten function explained 24.6% (AIC= -19.36), 32.07% (AIC= -33.25) and 37.02% (AIC= -43.48) of the variation of the data from these three nests.

Change in angular difference between outbound and subsequent inbound direction with age

When we examined the relationship between the angular difference in the outbound and subsequent inbound flight direction, and the age of the wasps using a generalized linear mixed model, we found that the angular difference increased significantly with age (estimate \pm s.e. of intercept 3.55 ± 0.11 , age 0.009 ± 0.002 ; z -value=3.69, $P<0.05$ for both intercept and age) (Fig. 9).

DISCUSSION

How the environment in which an animal evolves shapes its behaviour, including its foraging strategies, is a key question in behavioural ecology. For animals that evolved in a landmark-rich landscape, possessing familiarity with the foraging landscape can enable them to minimise foraging effort without affecting their foraging benefits; this can be of great advantage in natural contexts. In a previous study, we showed that foragers of the tropical social wasp *R. marginata* possess striking spatial familiarity with their natural foraging landscape (Mandal et al., 2017). This has also been shown in several other social insects (Collett et al., 2013; Narendra et al., 2013). Here, we investigated the ontogeny of the foraging abilities in *R. marginata*, and attempted to infer the relationship between the ontogeny of their foraging abilities and the development of their spatial familiarity with their foraging landscape. Instead of acquiring data from individual wasps throughout their lifespan, which would be ideal but is practically very difficult to conduct, we collected data for 3 days from foragers of various ages from three naturally occurring wasp colonies. Our results show that *R. marginata* foragers begin their foraging life by spending a substantial amount of time out of their nest for about 1–2 weeks without bringing any food back to their nest. The youngest wasps that started to make trips from their nest were within the first ~ 2 weeks of their lives. They began their foraging life with few short-duration trips and gradually increased the number of daily

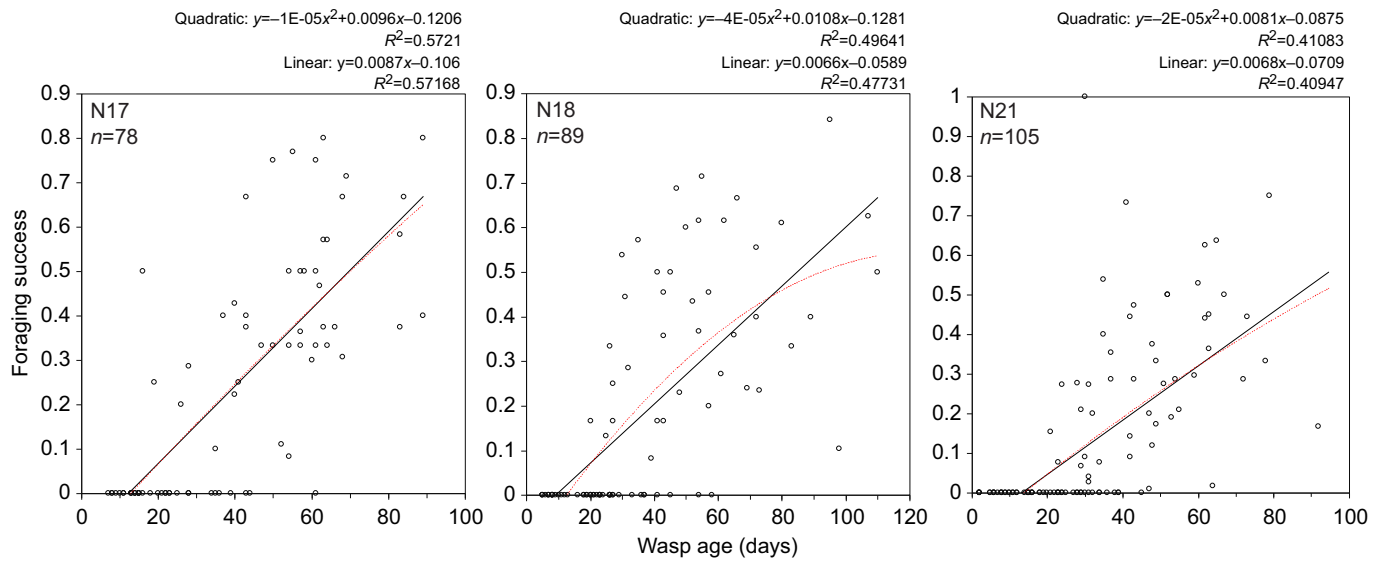


Fig. 5. Change in foraging success with age. Foraging success, calculated as the ratio of the number of trips in which the wasp brought food to the total number of trips made by the wasp, increased linearly with age ($P < 0.05$). (Linear model, black line; quadratic model, red line.)

foraging trips until about the middle of their foraging career, after which they began to take fewer trips; a quadratic function best explained the relationship between the number of trips they took per day and their age. During their initial foraging life, they also rapidly increased the average duration of their foraging trips and the total time that they spent daily on foraging. However, after about 4 weeks of age, their average foraging duration per trip and the proportion of time they spent foraging per day followed a gradual decrease, and they began to bring food. Thus, as they increased in age, they eventually reduced their foraging effort but increased their foraging gain. This indicates that wasps probably learn and memorise the location of food availability by acquiring sufficient spatial familiarity with their foraging grounds during their early foraging phase.

It is noteworthy that wasps rarely brought food to their nests during this initial foraging phase, although several wasps brought building materials and water. Compared with desert ants (Wehner

et al., 2004), honey bees (Capaldi and Dyer, 1999) and bumble bees (Osborne et al., 2013; Woodgate et al., 2016), which start bringing food to their nest when they are a few days old and after only a few trips outside of their nests (referred to as exploration flights/walks), the time *R. marginata* wasps took to start bringing food to their nest appears to be much longer. However, this is not surprising if we assume that wasps explore their foraging landscape to acquire spatial familiarity during their initial foraging phase, and the duration of this ‘exploratory phase’ can be attributed to the complexity of the foraging landscape and the distribution of the foraged materials. Compared with tropical insects like this wasp, the Sahara Desert ants, for instance, encounter fewer visual features to learn from their foraging landscape (which consists of occasional small bushes and minor variation on the surface of the land). This compels these short-lived desert ants to rely on the path integration system comparatively more than the learnt visual features of the

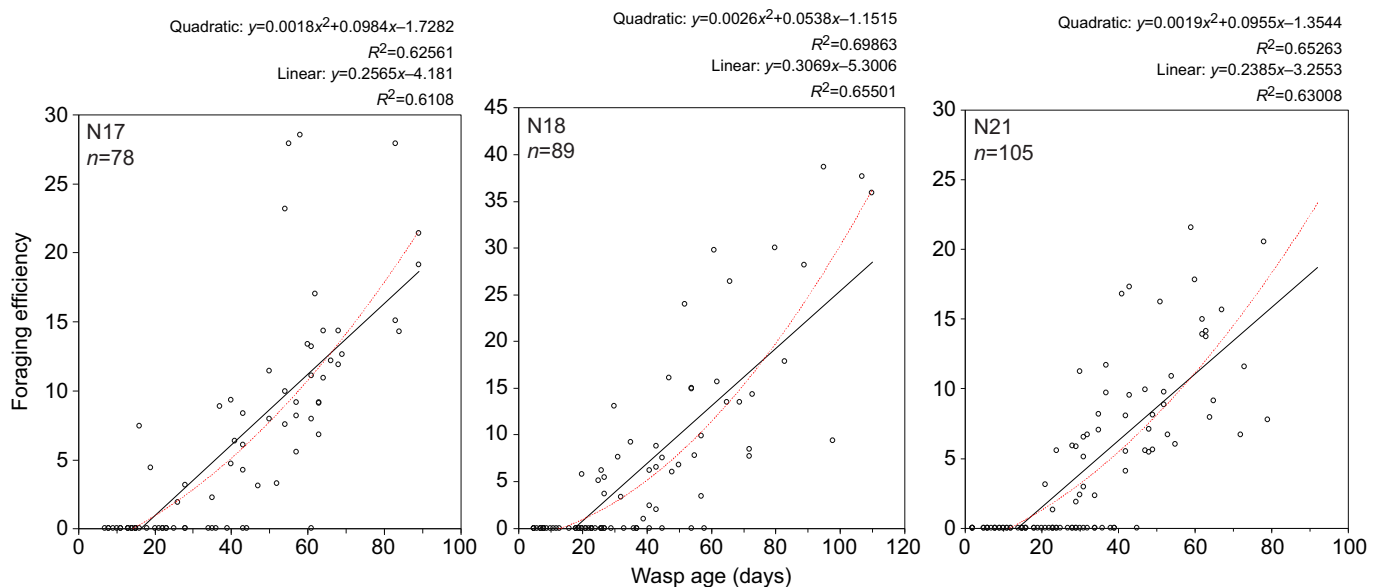


Fig. 6. Change in foraging efficiency with age. Foraging efficiency, computed as the number of times a wasp brought food to the nest divided by the proportion of time it spent outside the nest, increased linearly with age ($P < 0.05$ for all the three nests). (Linear model, black line; quadratic model, red line.)

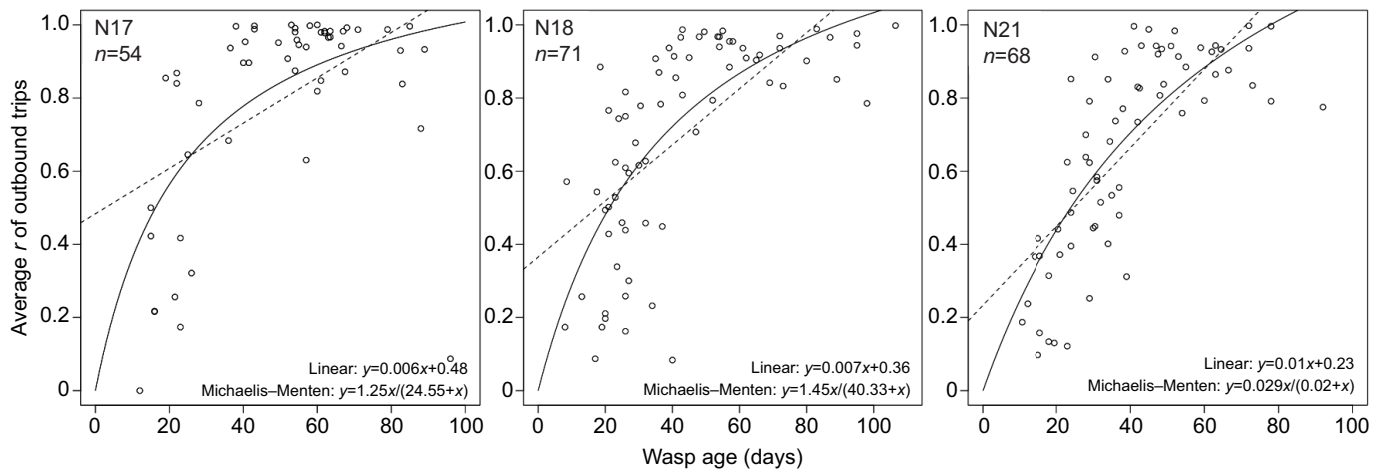


Fig. 7. Change in directional fidelity of foraging with age. Directional foraging, calculated by averaging the mean vector length of the outbound directions (r) shown by each wasp each day, increased with age following a Michaelis–Menten function (solid line): average $r=(A \times \text{age})/(B+\text{age})$. For all the values of A and B for all the nests, $P<0.05$.

landscape. Thus, once they get accustomed to being outside their nest, they can start foraging for food. The chances of encountering food, i.e. dead insects, may also be higher for these ants compared with the chances of tropical wasps finding camouflaged prey.

European honey bees and bumblebees have evolved in temperate landscapes that are more complex than the deserts but less complex than the tropics in which the *R. marginata* wasp has evolved. Also, bees forage to gather nectar and pollen from stationary flowers that advertise themselves to attract pollinators like bees, contrary to the mobile prey of the wasps that probably camouflage themselves to avoid their predators. Moreover, unlike *R. marginata* wasps, which practise solitary foraging, honey bee foragers can get information about rewarding patches from their nest-mates. Therefore, compared with the wasps, bees may start foraging for food while having much less familiarity with their foraging landscape; they may acquire the required spatial familiarity within a much shorter time, enabling them to start bringing food after just a few exploratory flights. Unlike the bees, a prolonged exploratory phase can be expected for a predatory

wasp that inhabits a highly dense tropical landscape and does not have the advantage of conspecific recruitment.

Ropalidia marginata individuals live for a much longer period and typically bring building materials or water before bringing food to their nest (Naug and Gadagkar, 1998). Such age-based polyethism has been reported in other paper wasps as well (Jeanne and Taylor, 2009). Building materials (i.e. plant fibres) are abundantly available throughout the landscape in the tropics. Thus, to collect building materials, wasps do not need to go to any particular place/direction, and foragers with very little or even no familiarity with the landscape can also accomplish this task. In fact, we found that the wasps that collected building materials were indeed among the youngest individuals of their colony, and showed no directional preference for their outbound trips. Compared with finding building material, finding a source of water may require more exploration, and bringing water repeatedly from the same place requires learning and memorising the location of the water source. We found that the water foragers performed several successful short-duration trips per day and the mean direction of

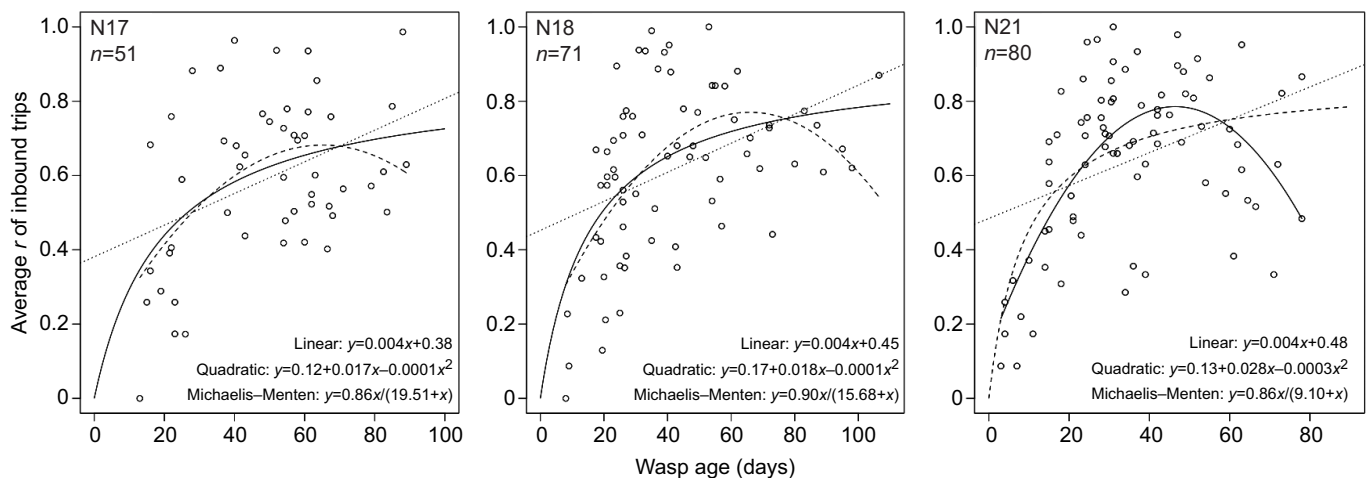


Fig. 8. Change in directional fidelity of inbound trips with age. The r -value of the inbound trips increased with age. Although slopes and intercepts of linear functions (dotted line) were significant ($P<0.05$) for all three nests, data from N17 and N18 were best explained by the Michaelis–Menten function (solid line; $P<0.05$ for all parameters), and data from N21 were best explained by a quadratic function (solid line; $P<0.05$ for all parameters).

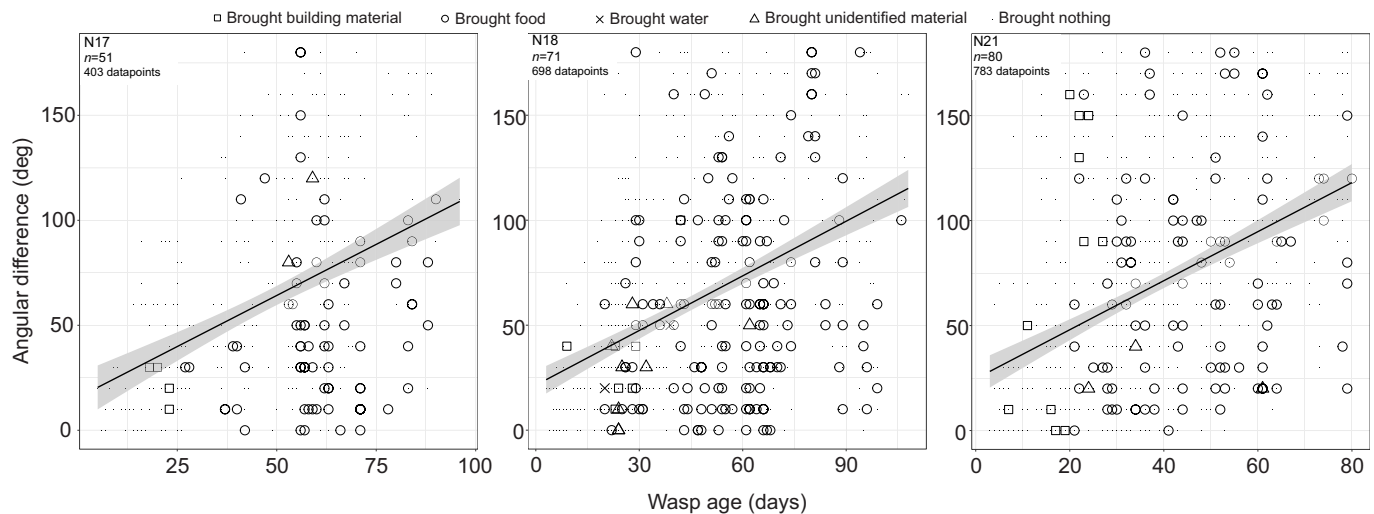


Fig. 9. Change in the angular difference between outbound and inbound direction with age. Angular difference increased significantly with age. The result is based on a generalised linear mixed model ($P < 0.05$, see Materials and Methods, and Results).

their outbound flights was towards the direction in which there was at least one permanent source of water (for instance, a fountain or a small water reservoir) within a distance of ~ 100 m from the nest. Wasps that brought food were among the oldest individuals of their colony. This may be because finding prey requires greater exploration, which may include visits to several places with the potential of prey availability. Thus, a thorough familiarity with the foraging landscape, which wasps may gradually acquire with age, might be essential for the wasps to forage for food efficiently.

A high investment to acquire spatial familiarity with the foraging landscape in early foraging life can only be balanced if the forager wasps can use that information to increase their foraging benefits in the future. Interestingly, we found that both foraging success (measured as the ratio of the number of trips in which a wasp brought food to the total number of trips that it took) and foraging efficiency (measured as the number of times a wasp brought food per unit time it spent on foraging) of the wasps increased with age. With increasing age, the reduction in foraging effort and the increase in foraging success and efficiency indicate their capability to learn and memorise the features of the landscape in their early foraging life, and to use this acquired spatial familiarity for efficient foraging later. This might be a stable strategy for predatory animals inhabiting highly dense landscapes. In contrast, desert ants (Wehner et al., 2004) and honey bees (Dukas and Visscher, 1994) also increase their foraging benefits with the advancement of their foraging life, but both of these insects do so by increasing their foraging effort; desert ants increase the number of foraging trips (Wehner et al., 2004) and honey bees increase their foraging speed and distance (from the hive) with increasing age (Capaldi et al., 2000).

We made an interesting observation during our study: several times, wasps took a long time (more than 2 h) to bring food from a foraging trip, and these were followed by a few, much shorter trips (within about 10 min) to bring food. We speculate that when they take a greater time to bring food to their nest, they may first find the prey by searching, then kill it and bring back a piece of it if the prey is large. For subsequent trips, they bring the remaining parts of the prey in the form of small pieces, and hence this takes much less time. Also, as their kills are lucrative food for several ant species, we speculate that the wasps might hunt for bigger prey when they are close to their nests, so that they can return quickly to the hunting site before ants claim the kill, but may kill only smaller prey (which can

be carried in a single bout) when they are far away from their nest. Testing these proposals could be an interesting future study to explore any relationship between spatial cognition and decision making in these wasps.

In a landscape where food is randomly distributed into patches, animals can achieve foraging competence by memorising the locations of rewarding patches and reaching those places directly on consecutive foraging trips (instead of searching for prey every time). We found that wasps indeed developed directional fidelity for the outbound flights with increasing age. The relationship between the consistency in their outbound direction and their age is best explained by the saturating Michaelis–Menten function. This suggests that the wasps fly in many directions during their early foraging period, probably for learning/exploring the features of the landscape (and therefore show less directional fidelity), but soon develop a preference for a particular direction, perhaps after encountering prey in that direction. Wasps may prefer to begin their search for prey in a direction in which they have encountered prey in the recent past, at least for some days. This indicates a development of spatial memory for rewarding sites in the experienced wasps.

As young wasps lack familiarity with the landscape, we expect them to rely heavily on the error-prone path integration system. As the degree of error increases with the directional/angular changes an animal makes during a foraging trip, we expected the naive foragers to take fewer detours during a single trip, and return from the same direction in which they flew during the outbound trip, as young honey bees are known to do (Capaldi et al., 2000). Consistent with this logic and the fact that young foragers did not show any directionality for their outbound trips, we observed a lack of directionality in their inbound flights as well. With increasing age, wasps increased the directionality of inbound flights, and the angular difference between the outbound and subsequent inbound flights. These results indicate that experienced foragers may forage by following a multi-destination trapline foraging route, as ants (Mangan and Webb, 2012) and bees are known to do (Buatois and Lihoreau, 2016; Lihoreau et al., 2012; Saleh and Chittka, 2007). However, following more than one trapline route may again reduce the directionality in the inbound trips. With age, wasps from two nests in fact showed an increase in the directionality of their inbound trips following the saturating Michaelis–Menten function, and wasps from the other nest showed an initial increase followed by a

decrease at older ages. As our data on the direction of the inbound flights were collected on the basis of the very last stages of the flight, this may simply indicate the best approach to the nest (and therefore might not be related to the actual foraging path). However, these results might also suggest that depending on the distribution of resources, which in turn depends on many factors including the landscape, wasps might develop one or more trapline foraging routes in different directions.

Conclusions

Our results show that individuals of the tropical social wasp *R. marginata* begin their foraging life by spending a substantial amount of time outside of their nest; they eventually reduce the number of foraging trips and the time they spend outside. With age, they show better foraging performance, and increased directionality for their outbound and inbound flights. The angular difference between the outbound and subsequent inbound flights also increases with age. These results indicate that these wasps perhaps acquire sufficient spatial familiarity with their foraging landscape during the early phase of their foraging lives. They probably do so by learning and developing a long-term memory of the features of the landscape. This memory, in turn, enables the wasps to reduce their foraging effort while still increasing their foraging gains. Such an ontogeny of foraging capability that is strongly influenced by the memory of their surrounding landscape acquired during their early foraging lives may be a reflection of their evolution in the landmark-rich tropical ecosystem.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.M.; Methodology: S.M.; Validation: S.M.; Formal analysis: S.M.; Investigation: S.M., A.B.; Resources: S.M.; Data curation: S.M.; Writing - original draft: S.M.; Writing - review & editing: S.M.; Visualization: S.M.; Supervision: S.M.; Project administration: S.M.

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Data availability

Data are available from the Dryad digital repository (Mandal and Brahma, 2019): [dryad.v116vr8](https://doi.org/10.5061/dryad.v116vr8).

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.199844.supplemental>

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