



Research article

Elucidating the daily foraging activity pattern of *Oecophylla smaragdina* to minimize bite nuisances in Asia large agro-system plantations

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ABSTRACT

Oecophylla smaragdina F., the Asian weaver ant, is one of the oil palm plantation's (*Elaeis guineensis*) potential predators, for the invasive bagworm species *Metisa plana* Walker, but this ant is a nuisance species that irritates plantation workers with their sharp bites. Here we assess the foraging activities (FA) of *O. smaragdina*'s major workers, identify its inactive times and the existence of supervision, a novelty for social insects. Between 2018 and 2022, the pattern of trunk foraging activity was used as a mitigation measure. The relationship between trunk FA and air temperature (AT), relative humidity (RH), air pressure (AP), and rainfall interception (RI) was also investigated. Our results showed that, *O. smaragdina* is a strictly diurnal ant species, has little to no crepuscular activity, and stopped foraging during darkness. Moreover, veteran bigger workers systematically acted as supervisors by monitoring trails, intercepting, and bringing back to nests smaller individuals during heat peaks. In relation to population size relative abundance, all colonies displayed greater intensity during the warmest daily periods with higher mean forager density among the bigger colony, regardless of the dry-rainy intervals corresponded to minimal activity from late scotophase to early photophase and showed a bimodal pattern. Thus, forager activity peaked between 1100–1530 h and 1745–1845 h, and an average two-fold daily sudden decrease in intensity between 1620 and 1650 h as a partial cut-off period (first report). Furthermore, foraging activity, AT, AP showed a significant positive correlation while RH was negative. Finally, we found that from the base palm trunks, defensive territorial layers extended to 5 m on average with different spatial configurations indicating greater foraging density within

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the first 2 m. Our study shows *O. smaragdina* daily low activity periods, before 1000 h, being the most suitable to avoid forager attacks to facilitate pruning and harvesting tasks.

1. Introduction

1.1. Arboreal activity

Oecophylla smaragdina (Fabricius) (Hymenoptera: Formicidae), a species of Asian weaver ants, is naturally arboreal and polydomous [1,2]. The colonies of this ant species inhabit numerous oil palm trees (*Elaeis guineensis* Jacq.), with multiple nests per palm, demonstrating intensive exclusively diurnal canopies foraging activity [3,4]. There are few publications on Asian weaver ants' foraging behavior, and the literature on *O. smaragdina*'s foraging behaviors is poorly documented [5]. Any movement from one location to another, such as from the nest to a distant target, is considered to be foraging, which is also known as "inward" and "outward" or "outgoing" or "returning" foragers [6]. The existence of individuals acting as supervisors to guide or monitor colony activity performance has never been reported in the literature for social insects, let alone for ants [7]. Further, besides *O. smaragdina* major workers' constant movements along the main access territorial entry (tree trunks), their daylight break periods have never been identified, yet revealed. This aspect is in dire need of an evaluation to provide answers in the literature. *Oecophylla smaragdina* and *Oecophylla longinoda*, African weaver ants, exhibit essentially identical hunting behaviors [8]. Any ant colony's safety and longevity depend on its foraging activity [2]. *Oecophylla smaragdina*'s foraging behavior is strongly influenced by the hunger levels of broods, adults, and foragers, which are the vector factors that trigger the search for food items [9–11]. Preys are transported back and stocked inside their nests [12].

1.2. Ground activity

The main workers can be seen actively foraging between oil palm trees, moving constantly with a few brief stops along the palm trunks toward the ground [3]. According to reports in the literature, weaver ants were observed constantly patrolling (during the time of bright daylight) with the widespread deployment of skilled major workers to protect the entire perimeter of colony territories [13]. Even when canopies are linked by nearby oil palm fronds [4], both *O. longinoda* [14] and *O. smaragdina* have frequently been observed actively foraging on the ground [15,16]. On the ground, *O. smaragdina* is known to create protective layers. These layers can be arranged in multiple groups starting from the base tree trunks and expanding further by numerous subsequent waves to create a few lines of defense [13]. In addition to the food's quality and amount, foragers' tactics should include solitary, tandem running, tandem carrying, group, and mass foraging [17,18]. The antennal sensilla interaction between at least two individuals is what is referred to as communication [19].

1.3. Biological control agent – bites nuisance

The Asian weaver ants have been used as a biological control agent in Vietnam [20], Southeast Asian citrus orchards (*Citrus sinensis* L. Osbeck), mango orchards (*Mangifera indica* L.) [21], and Australia cashew nuts (*Anacardium occidentale* L.) [22,23]. Both species of weaver ants have received more research attention in the last decade as biological control agents (BCA) [8,24,25]. Several significant obstacles stand in the way of weaver ants' potential for wider acceptance as BCA. It has also been recorded that *O. smaragdina* bites workers on cocoa (*Theobroma cacao* L.) plantations in an unbearably painful manner [26,27]. Due to this, the use of Asian weaver ants as a possible BCA was abandoned [25,28]. Thus, if weaver ants are to be used as a BCA, it will be easier to manage them and reduce discomfort for plantation workers if we are aware of and comprehend their foraging activity pattern. It is necessary to find solutions to stop or reduce the ants' constant attacks on plantation workers. The targeted quarantine defoliator *Metisa plana* (Walker) (Lepidoptera: Psychidae) has been causing severe foliar damage and productivity loss in oil palm plantations for many years [29,30].

The first goal is to predict a link between hourly foraging activity and seasonal foraging efficiency [31,32]. The activity pattern of ants may be affected by weather variables, such as atmospheric pressure (AP), air temperature (AT), relative humidity (RH), and rainfall interception (RI). *Oecophylla smaragdina* is categorically identified as a skilled daylight-dependent visual diurnal predator [33]. According to reports from previous studies [12,34], seasonal rainfall and climatic factors like temperature and relative humidity may affect the overall activity of *O. longinoda* [35]. The primary goals of this study were influenced by Peng et al. [5] assessment to determine the best daily hours for preventing *O. smaragdina*'s recurrent painful bite occurrences. To consider carrying out tasks on a plantation with the least amount of contact with these ants, we first look at which times of the day show less ant foraging activity. With the findings, plantation workers should be able to harvest fruit and prune fronds in peace during daily times of low ant activity in connection to weather parameters [5]. This will improve the likelihood of weaver ants being used as a BCA.

Then, we investigate *O. smaragdina*'s foraging activity patterns (diurnal, crepuscular, or nocturnal), and we look at the major workers' obvious aggressive behaviors, which suggest a promising potential to control dominant bagworms, similar to what has been observed for *Pteroma pendula* [3]. Three studies are presented in this paper; (i) Study 1 reveals the existence of any patterns in trunk foraging activity in connection to which the daytime period corresponds to the average lesser and higher number of active foragers. (ii) Study 2 identifies the daily peaks-lowest activity hours (defined as partial foragers cutoff period) by analyzing the trunk foraging activity pattern of *Oecophylla* major workers in connection to air temperature (AT), relative humidity (RH), air pressure (AP), and

rainfall interception (RI). (iii) Study 3 assesses the territorial defense boundaries of ground-dwelling foragers on wet and dry days. It is hypothesized that (1) beyond the labor division concept in ant, supervision by senior workers (bigger size) is performed on junior workers (smaller) during foraging activity due to high temperature/low humidity threshold presenting survival risk to these less heat resistant individuals. Even though *O. smaragdina* is a known intensive diurnal species, (2) it is expected to observe a partial break during the daylight period between activity peaks.

2. Materials & methods

2.1. Study sites

Through the agreement with Universiti Malaya (UM), field tests were approved by the Federal Land Development Authority FELDA and the Malaysian Palm Oil Board MPOB. The selected oil palm plantations are shown in [supplementary material Table 1](#). Oil palm plantations are established with a set of ecosystem functions consisting of similar fauna, flora, and microclimate environmental conditions nationwide in Malaysia [36] and Indonesia [37]. Hence, the comparative analysis was facilitated without any interference due to the absence of differences among diverse geographical locations. The data collection locations for the second focus study as depicted in [Figs. 1 and 2a-b](#) were located at Felda Gunung Besout in Perak, Peninsular Malaysia (03°50'04"N 101°17'48"E).

2.2. Weather collection data

The region has a year-round tropical climate characteristic of Malaysia, with daily air temperatures ranging from 18 °C to 36 °C. With a relative humidity mean daily minimum of 54% on the hottest days and a mean daily maximum of 97% in the early morning. The region experiences monthly rainfall fluctuation, with average monthly precipitation varying from 400 mm/month to 1000 mm/month. With typical microclimate zones in oil palm plantations, annual average mean temperatures and rainfall have shown substantial fluctuations over the decades [38,39].

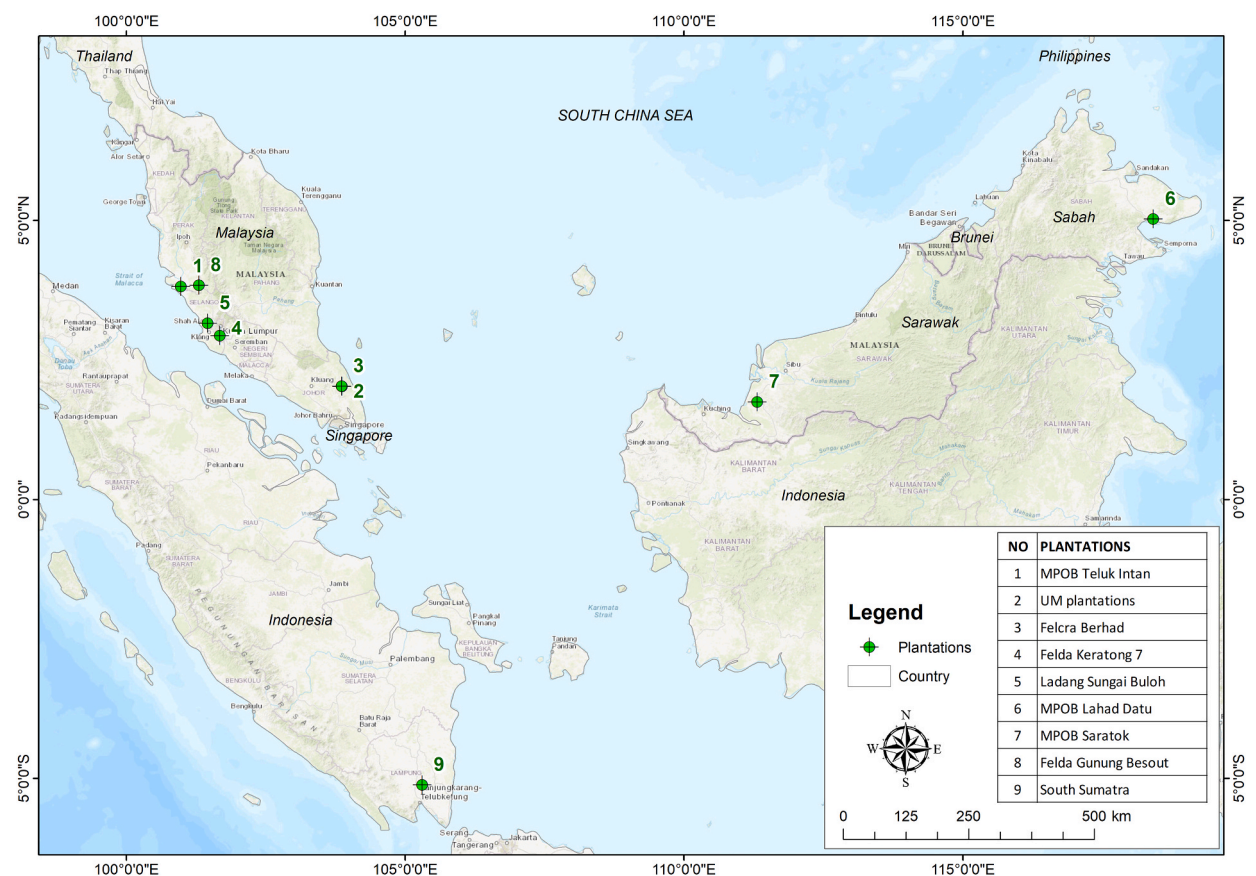


Fig. 1. Map location of the studied sites in Peninsular, East Malaysia Borneo Sabah-Sarawak and South Sumatra, Lampung Indonesia (selected oil palm plantations) as defined in the legends. The focus study is in Felda Gunung Besout Perak, North Peninsular Malaysia as shown in the legends. Source: Associate Professor Sr Ts. Gs. Dr. Khairul Nizam Abdul Maulud, Head, Earth Observation Centre, Institute of Climate Change, Universiti Kebangsaan Malaysia.

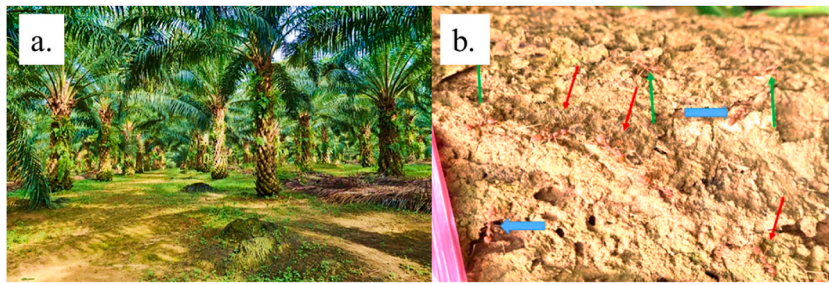


Fig. 2. a–b. Sampling sites of Felda Gunung Besout Perak oil palm plantations (a). Experimental setup in oil palm fields (b). Photo Credit (Moïse Pierre Exéllis).

The weather parameter data were obtained from three sources; (1) the National Meteorological Department, (2) an on-site weather monitor station (see [Supplementary Material Fig. 2](#)), and (3) galaxy sensors and a rain radar smart software on a portable Samsung Galaxy Note 20 internally equipped with measuring devices able to provide microclimate data at 1 m above ground level at a close distance from trunk and ground (≤ 1 m). The data records from the portable and weather monitor were combined because the data were comparable across the three recording methods ([Supplementary Fig. 3a-b](#)). The weather collection of data was conducted simultaneously and matched accordingly exactly at the time t corresponding to the average active foragers' number. For example at 1250 h, within 10 min of observations, the mean active foragers' records did correspond precisely to such environmental factors as air temperature, relative humidity, air pressure, and rainfall interception values. Along with forecasting on real-time maps using satellite images, it provided hourly data records on wind directions, cloud evolution, and rain forecasts. The Department of Irrigation and Drainage categorizes rainfall intensity per hour into light ($1 \text{ mm/h} \leq \text{RI} < 10 \text{ mm/h}$), moderate ($11 \text{ mm/h} \leq \text{RI} < 30 \text{ mm/h}$), heavy ($31 \text{ mm/h} \leq \text{RI} < 60 \text{ mm/h}$), and very heavy ($\text{RI} > 60 \text{ mm/h}$). This information is available at <https://publicinfobanjir.water.gov.my/hujan/>.

2.3. Data collection – analysis: clarification and caution

The way plantation management handles everyday maintenance and the harvesting of fresh fruit bunches (FFB) provides some key insights for the data collection technique. Employees of plantations carry out their tasks when there is no rain and the weather is clear and typical. Except for clouds and a brief time of light rain, which had no impact on their work stage. Thus, the majority of the data in these weather-clear field conditions were gathered. We specifically only include in our reporting individuals who meet the introductory requirements for being each colony's hunters and protectors (active major workers in motion).

2.3.1. Study 1: trunks foraging activity (time-nests abundance factors)

For this study, we define a bimodal foraging activity pattern as follows (foragers are only meant for major workers):

The presence of two daily activity peaks exhibited by active major workers with a corresponding significant decline in the average active foragers mean during the 24-h circle. During all the experimental design and monitoring of activity, the major workers are the only entity responsible for carrying out search and hunting tasks to collect food items for their respective colonies. Each colony is considered as a spatial replicate for all three studies and the major workers are the individuals being investigated only. Each colony represented a spatial replicate consisting of a sum of height. The foragers' activity was monitored over five years from 2018 to 2022 during dry (March–July) and rainy (October–February) seasons. This enabled to confirmation of the activity pattern similarity among the colonies, irrespective of the geographical location throughout the years: observations of continuous active foragers only during daylight periods. The plantation management confirmed the presence of *Oecophylla* mature colonies, at least 3 years old, deemed more appropriate for biological control treatments [40,41] at the time of data collection. We dissected a single nest per colony, to verify the presence of reproductive individuals attesting to the maturity level (see Ref. [42]). Hence all colonies were aged from 3 years and above for all experiments. Trunk foraging activity (FA) with their daily period: Since the main aim of this study is to find the best time of the day corresponding to the lesser forager active daily periods, each colony monitoring was carried out based on 24-h for 9 consecutive days. The detection of *O. smaragdina* colonies was done according to Exéllis & Idris [3] and Exéllis [4]. Preliminary monitoring was carried out on three colonies per plantation by selecting and tagging three occupied palm trees from each colony to carry out the monitoring of trunk foraging activity. We randomly set three 200 m transects along a path in the plantation to select three colonies per plantation. Each transect crossed the territories of at least one matured *O. smaragdina* colony. The antagonism test was performed to distinguish between different colonies. Ants from the same colony will pass and forage, and communicate with each other spontaneously, between released and resident ants. Ants belonging to different colonies will cause a fight [43,44].

The observation of each distinct palm was carried out following the experimental setting design shown in [Fig. 1](#). Shown are the major workers following moves in the trunk trail: ants leaving the nest or “outbound in red arrows”, ants returning to the nest or “inbound in green arrows”, ants functioning as supervisors at specific checkpoints on both sides of trails (blue arrows) exhibiting a slight bigger abdomen size. Three days of continuous observations every 2 h exposed similar activities of foraging patterns (activity is positive during daylight and absent upon sunset up to sunrise which corresponded to an inactivity period of around 2000 h–0700 h) for all 24 colonies (8×3). We define offensive foraging (OF) as a deliberate inner natural attitude leading the ants to search and kill a

multitude of insects to bring them back to the nests. Defensive foraging (DF) relates to the preventive and active behaviors deployed by the ants to prevent and stop any territorial perimeter intrusion. Night observations confirmed the complete absence of “OF” or “DF” behaviors under natural conditions. Without artificial physical interferences (i.e. manipulating the fronds, leaflets, touching or having fingers a few cm away from nests) forager guards did not detect any territorial encroachment, were just in a stand-by waiting attitude, exhibited only a very slow movement pace during the whole night up to dawn daily periods. Hence it is not feasible and accurate enough to detect all activities at the colony level without a time-lapse video recording system [45]. The slow motion and standstill attitude of foragers during night periods is not relevant to the aim of this study and the definitions and requirements given in the introduction for foraging activity hunting orientation. *O. smaragdina* is a known strictly diurnal species that does not demonstrate nocturnal hunting behaviors. Davidson et al [46] confirmed that *O. smaragdina* is a highly diurnal-predator leaf-forager species. Sometimes, there are still some foragers seen active on the ground after nightfall (any artificial source of light will ignite back their inner sense to move). In such cases, because some foragers, by exploring at a far distance from occupied trees, did not manage to come back on time before sunset; those foragers are trapped on the ground. *O. smaragdina* can never just be expected to behave like those ant species using pheromone trails for territorial navigation [33]. Observations done by night vision devices demonstrated their inability to move normally in daylight periods (impaired under darkness) and any detected movement under artificial light (torchlight) should not be confused with a normal foraging act (the observations given in lines 228–243 have never been reported before). Subsequent censuses were then performed only on a single palm tree per colony corresponding to a total of 8 palms for 8 colonies consisting of an average of 100 m² transect plots per each tree. Palm fronds were monitored every successive hour with the following observation schedule set up from 0700 h to 1900 h. The reading duration of activity was performed and standardized for 10 continuous minutes for each colony once every hour before the end of each period of observation. Since it became obvious that foraging activity (FA) is the task that exposes plantation staff to ant bites during frond pruning maintenance and harvest duties, another experimental design was done to further monitor *Oecophylla* foragers trails [5] on palm tree trunks only, consisting of major workers.

2.3.2. Study 2: foraging activity versus weather parameters

Based on the results of study 1 showing similarity in FA pattern among all monitored spatial replicates colonies (Supplementary Material Figs. 4 A-H, 5 A-H), this enabled us to focus on a single colony. The experiment on *Oecophylla* major workers foraging daily activity was carried out in the years 2020 (November–December), 2021 (January–February), and 2022 (April–June) at Felda Gunung Besout Perak. We aimed to identify FA patterns in relation to weather parameters (i.e., Air Temperature, Relative Humidity, Rainfall Interception, and Air Pressure). Upon verifying the beginning and end of daily foraging activity of *Oecophylla* major workers similar to a previous study (1200 h–1700 h and 1930 h–2330 h) [3], it was followed by a second phase of intensive monitoring to focus only on the positive daily activity period from 0700 h to 2000 h.

The number of ants foraging on the observed trunk was counted and recorded on an hourly basis 10 min before each ending hour time. All foragers leaving and returning to the nests were recorded. Secondly, FA peaks were subjected to detailed “micro” observations to detect the existence of any sudden mean active forager fluctuations. Peaks are defined as the mean taken from three replicated observations three times within a 24-h cycle [5,35] for three days each (total of nine days) made on a single trunk (Fig. 1). To obtain extra precision after the first expected more intense activity peak, 10 min observations were performed at 20 min intervals giving three readings per hour from 1600 h to 1900 h. This method facilitates the detection of sudden foraging fluctuations within short periods (3 h) during nine consecutive days. All ants’ external activities from the nests are considered positive while negative activity is confined inside their nests and palm canopies and/or when they stand in a stand-by mode along frond rachis and leaf surfaces.

During this experiment, the average daily period of weaver ant forager inactivity was identified. Monitoring was carried out for aggressive behavior between ants on palm trunks, fronds, and ground base trunks to identify interference from individuals of different colonies intruding on the experimental site. Previous studies indicated that individuals from different colonies will be aggressively fought by members of the colony [14,47]. Any detected ant(s) from other colonies were discarded from the records. To facilitate analysis, photos were taken 1 m around the middle of the trunk 5 min before the hour ended. In this manuscript, the terms foraging ants, *O. smaragdina* foragers, foragers, or *O. smaragdina* active ants are all exclusively meant for the major workers. Another objective of these field observations was to verify the necessity of using food bait during the foraging activity study. As proposed by Floren [48], Blüthgen & Stork [49], baiting is an effective way to attract arboreal ants to forage on the ground [50]. Food baiting was not necessary to survey and observe *O. smaragdina* colony’s activity in the present study since *O. smaragdina* foragers are permanently patrolling during the day in search of food resources [5].

2.3.3. Study 3: ground-dwelling foraging and territorial defense perimeter

To gather data on the colonies’ ground foraging activity schedule, three matured colonies (identified as colony I in Lampung Metro, Sumatra Selatan, Indonesia (2°56′11″ N 101°40′43″ E), colony II in Felda Gunung Besout Perak and colony III in Felda Keratong Pahang) were randomly selected and monitored during three consecutive days during dry and rainy periods. Random selection was performed by using the GPS Essentials software with a Galaxy Note20 S pen designating waypoints on the portable and Google maps by zooming in a surveyed *O. smaragdina* colonies occupied plantations section. Colony I, II observations were carried out during dry-rainy days of July–October 2022, November–December 2020, January 2021, and June 2022, respectively. Colony III was monitored from April to May 2022. There was no foraging activity under sustained rainfall occurrences continuously for 10 min, hence records were discarded. Supplementary Fig. 7 shows the experimental design conducted to collect the data. Preliminary observations were performed during 72 h from 0700 h to 1930 h to determine the activity peaks daily periods from 1000 h to 1800 h for all 3 colonies (average for 3 colonies). Supplementary Fig. 7 displays the main trunk trail (red arrow) in each observed nested occupied palm tree, splitting into three new distinctive trails (yellow, purple, and blue arrows) covering fluctuating angles ranging from an average of

90° to over 120° from the main palm trunk trail, estimated from the base trunks. The white arrows describe the first defensive layer at a 0 m distance at the base trunk exposing a higher density of *O. smaragdina* foragers around each occupied palm tree. The yellow, red, dark red, light green, dark green, and black circles represent the foragers' established defensive layers at 0, 1, 2, 3, 4, and 5 m distance from the base trunk respectively.

Three occupied palm fronds (having nests per colony) making 3 replicates for a total of nine monitored palm trees have been observed. Each palm consisted of $10\text{ m}^2 \times 10\text{ m}^2$ superficies transects representing 0.01 ha plot (0.03 ha per colony). After identifying the main trail, the collection of data was carried out by sampling a single palm per colony and consisted of counting each colony of the weaver ant ground-dwelling active individuals belonging to each respective occupied selected palm (Supplementary Material Fig. 7). The defensive layers consisted of five levels of 1-m width each, covering a fluctuating ground angle as depicted in Supplementary Fig. 7. All active foragers included within that surface were recorded. Any solitary, small groups or trails of foragers were counted within the palm tree radius average of 5 m [13]. Wandering weaver ants from the base palm trunks to the further ground surrounding territories (major workers) were recorded continuously during three days for 10 min every 2 h in the last quarter period (i.e., 1145 h; 1345 h). An alarm was used to signify the ending time of observations. For estimating the daily activity of ant colonies, any interference with foragers was prevented by avoiding the collection of food items. Photos were taken with visual identification of captured insects for record purposes. To estimate the territorial defense perimeter established by each colony around the occupied nest, a long open reel agricultural measuring tape (100 m) was used.

2.4. Statistical analyses

2.4.1. Generalized additive model GAM - cubic spline regression

We performed all statistical analyses for studies 1 & 2 using R version 4.3.2 [51]. We followed Durrleman & Simon's method to study the average foraging rate of ants as a function of time (and associated confidence interval). A cubic spline regression was implemented fitting a generalized additive model GAM model with Mixed GAM Computation Vehicle with Automatic Smoothness Estimation mgcv package with a cubic regression spline – a penalized cubic regression splines whose ends match, up to second derivative, and including time as a smoothing term. This method prevents the problems that result from inappropriate linearity assumptions [52].

225 samples were observed for each of the height spatial replicates (colonies), totaling 1800 samples of foraging activity.

2.4.2. Correlation - regression analysis – PCA

The foraging activity relationship (linear correlation) with the weather parameters (study 2) was analyzed using the Pearson indicator of correlation to measure the strength categorized as negligible, low, moderate, high, or very high with positive or negative directions of the linear relationship between two variables (Supplementary Table 2). The significant correlation between the two variables was determined at a significant level (α) of 0.05. The absence of multicollinearity was verified by Pallant's method [53]. By defining the Variance Inflation Factor (VIF), the multiple regression analysis was used to evaluate whether Air Temperature, Relative Humidity, Air Pressure, and Rainfall are related and affecting ants' foraging behavior. The multiple regression analysis was done to examine the relationship involving all independent variables (Air Temperature, Relative Humidity, Air Pressure, and Rainfall Interception) with the dependent variable (Trunk Foraging Activity) in a single model. Similar previous studies have used multiple regression in their examination [54–56]. We recognized a sample with a Mahalanobis space assessment surpassing its acute value of 20.52 [57]. This sample was removed. This is followed by a re-examination of the box and whisker plot to examine for any outliers. Four samples were found and removed. This is followed by a check on the residuals (errors) of the regression line to ensure the normality assumption is satisfied [58]. Additionally, the Kolmogorov-Smirnov and Shapiro-Wilk normality tests were performed to reinforce that the normality distribution of the dataset was achieved. Principal component analysis PCA was used to explore the dataset by identifying variables with different factor loadings (FL). The PCA of Pearson correlation was employed to examine the dataset pattern. It explored the correlation between all the weather variables of our study in a reduced factorial space. *O. smaragdina* activity was added as a supplementary variable. This means that activity wasn't taken into account in the calculation of the factorial space, but is visible in the PCA plots. Thus, the activity can be interpreted in relation to the weather variables. The analysis (PCA) helps to differentiate the amount of variance and importance within our set of abiotic variables in the habitat of the ants. It reduced the dataset expressively ($p < .05$) into smaller sets of new independent variables which are referred to as principal components (PCs). In this study, the PCA was executed, and cumulative variability (CV), eigenvalue (EV), and FL values were evaluated at a significant level (α) of 0.05. The factor loading (FL) range is as follows: $|0.00| \leq FL \leq |0.19|$ = negligible FL, $|0.20| \leq FL \leq |0.39|$ = weak FL, $|0.40| < FL < |0.69|$ = moderate FL, $|0.70| \leq FL \leq |0.89|$ = strong FL and $|0.90| \leq FL \leq |1|$ = very strong FL [59,60].

2.4.3. Colonies ground foraging activity differences

In study 3, to examine whether there are differences between ground foraging activity and defensive lines between Colony I, II and III, a one-way between groups analysis (ANOVA) is performed with the Robust Tests of Equality of Means to verify the appropriate homogeneity of variance. Finally, a Post-hoc comparison using the Scheffe test was performed.

3. Results

3.1. Study 1: average trunk foraging activity as a function of time

Fig. 3 is a graphical representation of all weaver ant foragers pooled activity according to the time of day, including the study of the average activity (and the 95% associated confidence interval in distinctive shaded colors) using a “cubic spline” regression. This shows a bimodal distribution pattern with two daily activity peaks and the absence of nocturnal active foragers as defined in Section 2.3.1 of the methods (first and second peaks in black brace – activity decline pointed by red double side arrow). Data for each replicate (colony) are represented by different colors. The blue smooth curve line proposes a model representing the cubic smooth regression of the average number of ants independently of the replicate (colony). The shaded area surrounding the curve represents the 95% associated confidence interval.

Regarding trunks' daily foraging activity with the height colonies' spatial replicates by nest abundance, all height replicates under monitoring exposed similar bimodal distribution in activity patterns throughout the year in the absence of rainfall. This corresponded to an average of 22,977.00 foragers ants monitored during 1728 h (mean of 2857.00 ± 500 ants/hour during active peak hours for 72 days; hence a mean of 40 ants/hour/day ± 5). Based on the data recorded, it is suggested that the number of foraging activities increases by daylight and abruptly decreases when reaching dusk. Fig. 3 shows the individual observations made on the number of trunk foragers according to time by the height replicates (colony). All observed populations exhibited foragers taking the highway trunks at later hours of the day when the sun is high by 0930 h on average to return to their nests upon sunset irrespective of the seasons (dry and wet periods of the year).

An increase in the mean daily foraging activity with the increase of total nests per distinct replicate (colony) was manifest from various geographical locations in Peninsular and Borneo Malaysia (Supplementary Fig. 5I a–c). The Pearson Correlation Coefficient values $r = 0.94$, $r = 0.95$ with the coefficient of determination ($R^2 = 0.89$ and $R^2 = 0.90$), is a strong positive correlation between the mean foraging peak and the mean trunk foragers with each replicated colony nest abundance, respectively. The result is significant at $p < 0.00001$ (Supplementary Fig. 6a–b).

It is worth noticing that during the peak foraging period corresponding to the hottest time of the day, larger foragers increased among the individuals in all trails. Fig. 4 shows a larger major worker transporting back a smaller intermediate-size worker picked up from the ground back to the nest during higher daily air temperature (1200–1500 h) at Felda Keratong Pahang. Fig. 4 shows a close shot of this extraction from the trunk trails of workers transporting them (polymorphic size workers – large, intermediate, and minor) systematically back to the closest located nest under the shade of a more tolerant temperature. The mandibles are seen holding the abdomen side gently with no crushing pressure applied (black circle & black arrow). The occurrence of this leading supervision from bigger size-darker major workers by intercepting acts of vulnerable workers happened always within the trunk and base trunk zone only.

3.2. Study 2: trunk foraging activity pattern in relation to environmental factors: correlation

The variations in foraging activity throughout the day demonstrated an increase to a maximum level at an optimum temperature of 28 to 33 °C while it was significantly reduced by cold temperatures at the highest relative humidity. See Supplementary Table 8 to view the combined dataset showing records of study 2. *O. smaragdina* exhibited a short period (average 30 min to 1-h maximum) of dramatic decrease in foraging pattern daily activity with two peaks (Fig. 5a–b). The first peak occurred around midday (1100 h–1530 h) and the second peak around dusk (1745 h–1845 h). The majority of foragers on their way back to the nests by sunset exhibited much slower movements in the trails. There is a transition period duration of an average of half an hour before a total ceasing of their activity. This corresponded to the crepuscular and dusk daily phase. Hence if the sunset occurred by 1930 h, the lower activity would correspond to approximately 2000 until around 0700 h corresponding to the scotophase day period (Fig. 5a–b). The average number of active ants during the peak hour is an average of 5–10 folds compared during the ebb with a peak average of > 25 ants ± 5 ; the ebb average is equal to 1 ant (rainy days) and 2 ants (Dry periods, $N = 432$ sampling observations). Overall, *O. smaragdina* demonstrated intense activity as early as 1000 h until 1500 h corresponding to the photophase daily period with a sudden sharp short periodic decrease of 12 ant foragers by 1620 h–1650 h (see Supplementary Table 8), and back to 25 ants until 1900 h (marking the end of the daily photophase) to decrease dramatically by the end of the crepuscular and dusk period. This decline in ants' activity coincides with the decrease in air temperature and increase in relative humidity and light absence during each nocturnal daily phase confirming the Asian weaver ant as a strictly diurnal active species. Two transition activity periods could be identified as follows: in the early morning by sunrise up to 0830 h (starting) and by sunset up to 0800 h (ending). Supplementary Table 8 shows the average means of active *Oecophylla* major workers in relation to AT, RH, RI, and AP in Gunung Besout plantations. There is a similar bimodal daily foraging pattern in both seasons regardless of foragers' activity intensity fluctuations between dry and rainy seasons. All observations carried out during sustained rainfalls indicated, which does take place during dry and wet seasons, absence of foraging activity (see supplementary raw dataset study 2), considering that relative humidity (RH) increases with more rainfall interception (RI). During sustained rainfall, the foragers cease all activity outside their nests. The graphic analysis (Fig. 5a–b) shows that the ants have two peak, intense active periods when their foraging activity is at least two times higher than during the inactive phase during the rest of the year.

The correlogram Fig. 6 shows the Pearson correlation coefficients and significance tests for the variables. As seen in the table, there are positive and negative correlations between the variables. The strongest negative correlation was between the Air Temperature and Relative Humidity ($r = -0.9$, $P < 0.01$), while the lowest correlation was between Air Temperature and Rainfall Interception ($r = 0.52$, $P < 0.01$). Significant negative correlations were found between Relative Humidity and Air Temperature ($r = -0.9$, $P < 0.01$), Rainfall

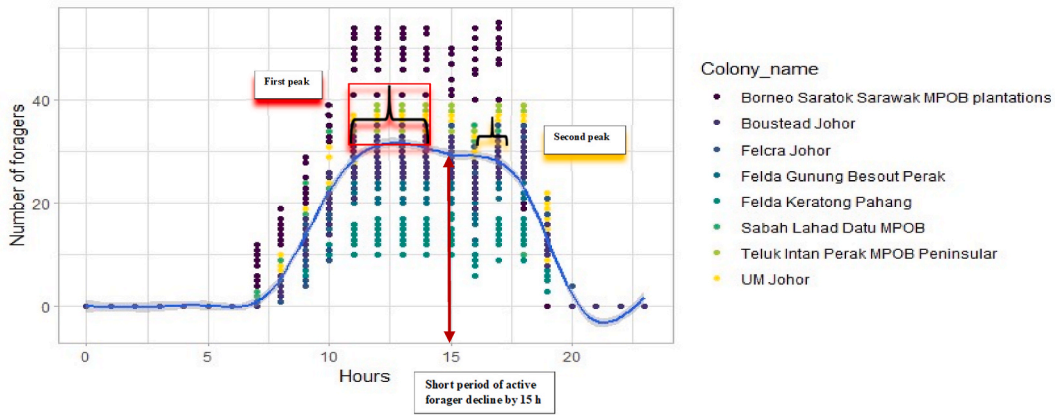


Fig. 3. Number of foraging ants versus time. The blue curve exposed a daily bimodal foraging distribution pattern with two peaks (1100–1500 h and 1745–1845 h on average) with a short period of decline in foraging intensity between after 1500 h.



Fig. 4. Bigger size major workers control, and regulate foraging activity demonstrating exceptional leading supervision function never reported for social insects. Photo credit: Exéllis Moïse Pierre.

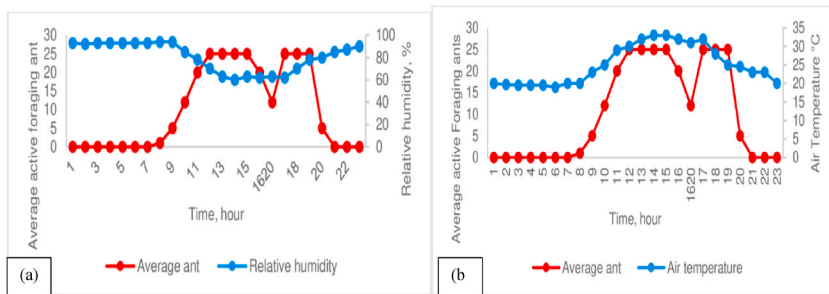


Fig. 5. a–b. Graphs of daily foraging activity in relation to AT (a). Graphs of daily *O. smaragdina* major workers foraging activity in relation to RH (b). a–b shows a clear foraging bimodal distribution pattern with more accuracy: two peaks from 1100 to 1530 h and 1645–1900 h with a short period of decline in between around 1620 for an average of 30 min.

Interception ($r = -0.6, P < 0.01$), Air Pressure ($r = -0.85, P < 0.01$) and Foraging Activity ($r = -0.86, P < 0.01$). The presence of a high correlation between the variables, as the case in the correlation between Air Temperature and Relative Humidity, could indicate the presence of a multicollinearity issue. After an examination, all VIF values were below 10 which indicates that multicollinearity was not a problem. Additionally, all Tolerance values were above 10, which also indicates that multicollinearity was not an issue.

3.3. Regression analysis - PCA

The regression analysis’s findings showed that the four (4) predictors accounted for 82.4% of the variance ($R^2 = 0.824, F(4, 66) = 83.000, p < 0.000$) (Table 1 is a summary of the causal links among the variables that were evaluated using regression analysis). We found that beta values for AT, RH, AP, and RI which were obtained, are 0.317 with a significant p-value = .001, -0.775 with a p-value

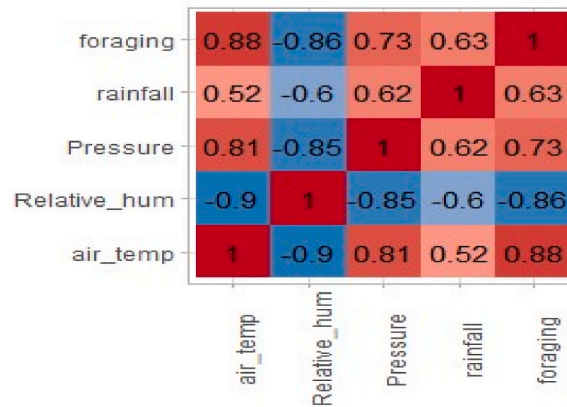


Fig. 6. Correlation plot of Person correlation of the dataset variables.

= 0.001, -0.236 with a p-value of 0.002, 0.131 with a p-value of 0.007, respectively; the findings imply that the positive association between air temperature, relative humidity, air pressure, rainfall interception and foraging activity is supported by the data. The beta coefficients are utilized in the regression analysis to illustrate how important each of the four independent variables was in terms of their contribution to the variance inflation factor (VIF) in trunk foraging activity. According to the findings, relative humidity ($B2 = -0.775$, $p = 0.000$) carried the heaviest weight, followed by Air Temperature ($B1 = 0.317$, $p = 0.001$) (see Figs. 4 and 5a-b), Air Pressure ($B3 = -0.236$, $p = 0.002$) and Rainfall Interception ($B4 = 0.131$, $p = 0.007$).

Principal Component Analysis Scree plot (Fig. 7a) highlights the two first factorial axes that account for more than 93% of the dataset's total variability. Thus only these two axes are represented with a biplot (Fig. 7b). In the biplot, the foraging arrow points in the same direction as air temperature and pressure so these variables are all correlated, on the other hand, these three previous arrows point in the opposite direction of relative humidity, indicating that high relative humidity is harmful to the activity. The rainfall arrow, which is almost at a right angle with foraging, indicates that precipitation has no relationship with activity (Fig. 7a-b). Table 1 shows that only PC1 explained the underlying factor that affected the number of foraging ants by FL of $|0.700| \leq FL \leq |1.000$ (AT, RH, AP, and RI) which explained 84.01% cumulative variability (CV) of the dataset.

3.4. Study 3: ground-dwelling foraging and territorial defense perimeter

Generally, foragers proceed to a massive withdrawal from the ground towards the trunks and come back to their nests at the lowest AT corresponding to the highest RH records. This behavior was usually seen during sustained moderate or heavy rainfall and by the end of the crepuscular and beginning of the dusk period. Monitoring the daylight activity exposed the tendency of ground-dwelling foragers for long periods from an average few hours upon sunrise up to sunset descending from their respective nests through the trunks to explore more territories for food hunting purposes (Fig. 8A–D). Fig. 8 exhibits arboreal Asian weaver ant major workers in contrasting long-period behavior ground-dwelling activity. Daily trails on the ground from the palm base trunk spread further up to a 3–5 m radius around each occupied palm tree having nests (Fig. 8A). Weaver ant aggregation on the ground without trails is a common sight during the daily active peak hours (Fig. 8B). Ground foraging activity is established by defensive layers' spatial arrangement (Fig. 8C). Fig. 8D shows the ground-dwelling solitary forager capturing insect food items. Territorial monitoring is carried out solely by major workers and involves the coverage of all inhabited habitats, including palm canopies, brood nests, barrack nests, trunks, fronds-rachis, base trunks, and the ground.

Major workers established a defensive perimeter layer to protect any non-colony members from encroaching into their territory. All defensive perimeters established per colony featured average layers distance from 0 m to 5 m from the base palm trunk (the distance between each palm tree is an average of 10 m for all plantations). All colony territories include distinct, well-organized "checkpoints" (Supplementary Fig. 7, blue arrow), where larger, darker workers can be seen supervising others. Throughout the long, hot days, foragers from different colonies would frequently engage in violent conflicts when passing across one other's territories. The alien individuals barely manage to cross over the defensive layer, facing a prompt collective attack from each colony's vigilant guards.

To examine whether there are differences between ground foraging activity and defensive lines between Colonies 1, 2 and 3, a one-way between groups analysis (ANOVA) is performed. 144 samples were observed for each of the colonies, totaling 432 samples (Supplementary Tables 12, 13, 14). There was a statistically significant difference at the $p < 0.05$ level of foraging activity and defensive lines for the three colonies: $F(2, 429) = 22.833$, $p < 0.05$. While reaching statistical significance, the actual difference in mean scores between the groups was medium [61], (p . 284–7). The effect size, calculated using eta squared,¹ was 0.09. The Robust Tests of Equality of Means show that the assumption of the homogeneity of variance is corrected and not violated (Supplementary Table 12).

¹ Eta squared = Sum of squares between groups/Total sum of squares.

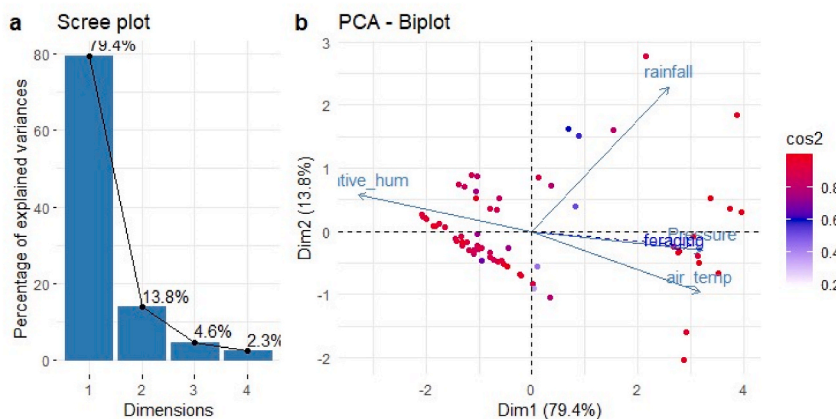


Fig. 7. a–b. Principal component analysis of the dataset covariates: Figure a represents the screeplot and b represents the biplot (individual and variable plot) with the number of foraging ants added as the supplementary variable.

Table 1
Principal component analysis PCA.

Variable	Principal component (PC) ¹	
	PC1	PC2
Time, h	−0.1393	0.9665
Air temperature, °C	−0.9294	−0.1417
Relative humidity, %	0.9522	0.0924
Air pressure, hPa	−0.9027	−0.0706
Rainfall, mm/h	−0.7394	0.2551
Average mean active ants' foragers number	−0.9244	−0.0431
Eigenvalue (EV)	4.0060	1.0346
Percentage variability (PV), %	66.7668	17.2440
Cumulative variability (CV), %	66.7668	84.0108

Note: ¹ $|0.000| \leq \text{FL} \leq |0.300|$ = weak FL, $|0.300| < \text{FL} < |0.700|$ = moderate FL, and $|0.700| \leq \text{FL} \leq |1.000|$ = strong FL.

Post-hoc comparisons using the Scheffe test indicated that the mean score for Colony 1 ($M = 9.90$, $SD = 11.19$) was significantly different from Group 2 ($M = 4.43$, $SD = 6.06$) and Group 3 ($M = 4.22$, $SD = 5.89$). Colony 2 and Colony 3 did not differ.

Correlation analyses were done to assess the strength of relationships between the defensive lines of Colony 1, 2, and 3. [Table 2](#) determines that there are positive substantial connections between the defensive lines in Colony 1, except between defensive lines 3 and 5. [Table 2](#) and [Supplementary Table 12](#) also demonstrate that there are three (3) positive important associations amid the defensive lines in Colony 2. Defensive line 4 of Colony 2 could not be calculated as the data were recorded as null (0). [Table 2](#) validates that there are only four positive major relationships between the defensive lines in Colony 3 (*the mean difference is significant at the 0.05 level). Defensive lines 4 and 5 of Colony 3 could not be calculated as the data were recorded as null (0). Overall, [Fig. 9a-b](#) shows the difference in mean ground foragers between the three colonies at a 95 % confidence interval (CI) by superiority level in favor of colonies 1, 2 then 3.

[Fig. 9a-b](#) represents the clustered bars for colonies 1, 2, and 3 in blue, red, and green respectively.

During surveys and censuses in Lahad Datu, Sabah an exceptional event occurred as a consequence of an invasive sampling of a dealate queen nest. The sight of a massive emergency response from extremely aggressive major workers protecting the colony gravid queen by performing an evacuation exhibiting a fast-moving compacted aggregation on the ground was astonishing. The response shown by major workers during an emergency defense of their gravid queen is exceptional (see [Supplementary Material Fig. 8](#)).

4. Discussion

The study investigated the major worker trunk foraging activity patterns (diurnal, crepuscular, or nocturnal), in function of the colony size (expressed by colony canopies nest number) and detected the daily periods corresponding to the lowest and highest number of active foragers. The peaks-lowest active hours were further analyzed in connection to air temperature (AT), relative humidity (RH), air pressure (AP), and rainfall interception (RI). Ground dwelling foragers' territorial boundaries were identified to expose the Asian weaver ant spatial occupation strategy.



Fig. 8. (A–D). *O. smaragdina* Ground foraging activity. Photo credit: Exélis Moïse Pierre.

Table 2
Multiple Comparisons for ground foraging activity.

Dependent Variable: Ground Foraging Activity						
Scheffe						
(I) Colony	(J) Colony	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Colony 1	Colony 2	5.47222 ^a	0.95398	0.000	3.1290	7.8155
	Colony 3	5.68750 ^a	0.95398	0.000	3.3442	8.0308
Colony 2	Colony 1	-5.47222 ^a	0.95398	0.000	-7.8155	-3.1290
	Colony 3	0.21528	0.95398	0.975	-2.1280	2.5585
Colony 3	Colony 1	-5.68750 ^a	0.95398	0.000	-8.0308	-3.3442
	Colony 2	-0.21528	0.95398	0.975	-2.5585	2.1280

^a The mean difference is significant at the 0.05 level.

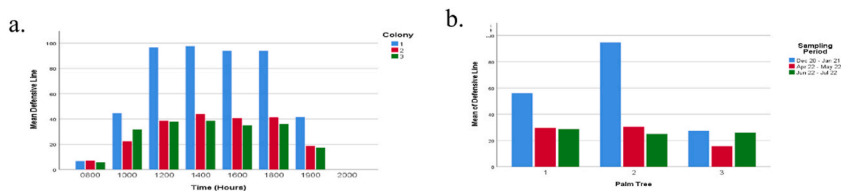


Fig. 9. a–b. Mean ground forager defensive line in relation to time and colony (a); mean ground forager defensive line in relation to palm tree and sampling period (b).

4.1. Trunk foraging activity in relation to colonies' nest abundance

O. smaragdina is widely distributed and mobile, two traits that firmly support any effort to understand the nuances of the species' complex foraging behaviors [2,62]. The effectiveness of ant collective foraging is primarily dependent on information being exchanged between nest members through antennal interaction and pheromone emission [63]. Our research can suggest a substantial and organized relationship between tactile communication and the use of visual aids by *O. smaragdina* foragers (an established intrinsic behavior) while they are engaged in an activity. Ogawa et al study's [64] defined the strictly oriented daylight visual hunter behavior

(see the flicker fusion frequency and its critical associated factor to understand the fast temporal resolution sight found in *Oecophylla* major worker which is closely similar to flying insects, i.e. bees/flyes). In line with several studies [65,66], the observation of larger major workers increasing in foraging trails during daily temperature peaks indicated that they had better heat tolerance at higher temperatures than the more vulnerable smaller size workers. The present findings contrast with the never reported existence of individuals acting as leaders to supervise-monitor colony workers during foraging activity, which normally does not apply for social insects in general, yet for any ant species [7]. This defies the stigmergy universal mechanism concept known for ants [67]. The act of removal of smaller more vulnerable individuals systematically during the hottest daily periods, from the trunk-ground trails veteran workers, is suggested to be a preventive behavior from high potential lethal dehydration risk. According to some studies [68,69], ants may become stressed or injured by thermal circumstances that are outside of their comfort zone. The existence of three intermediate-size workers, with their precise distinct measurements, besides the major and minor has been reported recently and shows a diversity of foragers' sub-caste [70].

The seasonal average temperature range in the present research generally shielded weaver ant foragers from critical foraging thermal limits that might have led to a high mortality rate, as was demonstrated in another study on the global distribution scale for different ant genus [69]. Lasmar et al. [71] found a correlation between foraging activity and the number of ant workers in the colonies. Additionally, colonies alter their foraging activity in response to a collective decision-making process that is governed by daily periods and population abundance [69].). By observing the daily shifts in "locomotor activity" of ants to changing temperatures, this information can be used for integrated pest management or biological control strategy against the quarantine bagworm defoliators *Metisa plana* in oil palm plantations [29,30,72]. This action may be less likely to result in weaver ant bites if it is properly matched or tailored to the plantations' pruning and harvesting tasks.

4.2. Influence of weather parameters on weaver ants' daily foraging activity

The overwhelming majority of ant species' foraging activity occurs between the temperatures of 10 °C and 45 °C [7]. According to Hölldobler & Wilson [7], daily variations in surface temperature are one of the main factors that regulate ants' behavior. As a result, the atmospheric temperature for arboreal species like the genus *Oecophylla* is thought to be important. Another research found that the number of foragers significantly decreased and eventually stopped foraging when the air temperature fell below 12 °C [73], which corresponds to the critical foraging thermal minimum range [69]. According to Peng et al. [5], *O. smaragdina* foraging activity was influenced by temperature, with lower temperatures in the morning and late afternoon being associated with higher activity levels, while higher RH levels were associated with lower activity levels. While the AT values for weaver ant activity strongly disagree with the results of our research, they substantially agree with those for relative humidity.

It was suggested that the lower time of the daily activity pattern, which corresponds to a less aggressive time, be used to reduce *Oecophylla* ant bites, but physical commotion may encourage attacks, which is supported by a second evaluation done on cashew nuts [47] in Australia. *Oecophylla smaragdina*'s efficient foraging behavior is linked to relatively high air temperature and pressure, which are decided by moderate and strong correlations, respectively. Our results closely resemble those of the African weaver ant *O. longinoda*, which was observed in Zaire and Cameroon between 0900 and 1700 h every day with no decrease in activity during the hottest part of the day [74]. In contrast, (Peng et al. [5] showed that ant activity decreased during the hottest part of the day. However, Peng et al. [5] report supported this study's discovery of two activity surges during the day, one of which occurred between 1600 and 2100 h and the other occurring between 0800 and 0900 h. In contrast to our approach, Peng et al. [5] assessed ant activity at the colony level by observing four tasks (foraging, surveillance, communication, and brood transport).

O. smaragdina major workers in oil palm plantations showed a pattern of response by usually returning to their nests with relative humidity increase [5]. Both the stated weather conditions and the abundance of inside nests may exert some degree of coercion on one another. However, this does not necessarily imply that nest humidity is more strongly influenced by the number of ants in the nest rather than by the external environment. In a similar manner, Gordon et al. [6] claim that for the harvester ant *Pogonomyrmex barbatus*, food availability and some other ambiguous variables are more important predictors of foraging activity than humidity alone. These main variables are desiccation impact, olfactory receptors variation among colonies, the nature of the foliage in which major workers are exploring to find a food chain supply, the flow in terms of workers' abundance, frequency of successful forager transporting resources back to the nest [6].

Our findings essentially imply that forager behavior is affected by AT, AP, and RH. The daily monitoring of soil temperatures and relative humidity fluctuations influence enforced such findings by uncovering the major workers' similar foraging activity patterns demonstrated in this study (Exéllis, unpublished data).

4.3. Ground-dwelling activity, territorial defense

When examining their possible biological control relationship with agricultural pests, foraging activity studies of grown-dwelling ant species are of economic interest [75]. This research corroborated Offenberg's [15] findings that *O. smaragdina* foragers are spending longer daylight periods guarding, exploring, and hunting over a larger perimeter away from the occupied central canopies of palm trees.

Similar to the results of Lim [13] in mahogany plantations, the task force of experienced major workers established an average 5-m defensive layer around the base trunk of all occupied palm trees. *Oecophylla* ants were able to detect human presence at a distance of 5 m, according to Lim [13]. The current study demonstrated the ferocity with which major workers foragers deal with intruders and other weaver ants from various colonies, demonstrating the risky nature of foraging and colony defense and the consequently high

mortality rates in ants [76]. When a colony extends its range by engaging in initially intensive foraging activity to find appropriate new areas, the same territorial defensive approach is consistently used [7]. Such interactions with weaver ant colonies could cause a burned effect on the leaves as a result of the release of formic acid [7]. Similar to this, the major workers are especially devoted to their defense of the colony's founding queen (see [Supplementary Fig. 5 S5](#); this photo capturing the act of queen protection is the first ever provided online). Unknown is the colony queen's defense strategy. An evacuation by retinue exercise is what it is known as [77]. A large number of extremely aggressive veteran troops who are larger than others and are supported by smaller workers are gathered around the queen, who is in the middle of that quickly moving ball type. A queen requires workers' assistance to move in a vertical orientation because she is too heavy and has underdeveloped arolia [78]. This safety procedure stops the queen from blowing her delicate abdomen when she falls [77].

Additionally, studies on the foraging behavior of weaver ants showed that any experimental method design is dependent on the purpose and goals of the research; for example, working within ant colonies nearby habitats to observe different foragers [5]. In contrast, different research made use of a technique that was farther from the primary site of occupied trees, including extensive ground-dwelling weaver ant monitoring [79]. The *O. smaragdina* territorial arrangement reflects the greater demand for resources to accommodate brood development. The increased ground-dwelling activity that accompanied colony growth was caused by more bug prey becoming available during the monsoon rainy seasons of the year [80]. The effective protection services offered by weaver ants can be attributed to a mix of a wide range of foraging activities spanning inhabited areas and systematic predatory behaviors towards many insect pests in agro-systems with *O. smaragdina* [8]. By gathering data from African and Asian nations that have adopted weaver ants as a pest control tool, Van Mele et al [28] provided a thorough practical protocol study on the proper management for managing *Oecophylla* ant bites nuisance. In the instance of weaver ants, the concept of using the morning's cool temperature to correspond to the day's lower foraging activity levels was already in use [81]. Combining this with the periods of consistent, heavy rain that cause foraging activity to stop could reduce the annoyance of bites during plantation maintenance and harvesting tasks. Since microclimate is more important than macroclimate in determining ant foraging patterns, more research on foraging behavior in connection to data is required. For instance, in the rainforest ant community, the temperature of each colony and its tree varies, affecting the ant's thermal performance and influencing whether or not worker ants go foraging [82]. It is suggested to look into possible effective predation on the dominant and seriously harmful invasive bagworm species *M. plana* producing losses and recurrent infestation. This could reduce the dependence on wide-spectrum contact long-range harmful chemicals (cypermethrin used as a standard treatment) highly toxic and harmful to non-target taxa and humans, i.e. pollinators [83] thus their removal would promote environmental restoration. Further, Davidson et al [46] demonstrated that a majority of ant species hunt for an easy target to reduce energy cost consumption, hence choosing a scavenging search orientation to bring food supply back to the colony. In contrast, *O. smaragdina* is a visual daylight hunter of living prey: this behavior is important for the biological control of invasive species of bagworms like *M. plana*, by offering to at best abolish toxic pesticide dependence. This ecosystem service might function effectively to prevent the loss of non-target taxa insects many could be beneficial. The broader ecological implication is a contribution to biodiversity conservation in the long term with the perspective of adopting such a highly active functioning natural enemy [87], hence having a potentially significant impact on the environmental safety level of such a large monoculture industry of Southeast Asia [29,30]. The selective promotion of more effective pollinators such as the bees *Xylocopa* spp. (bigger size) is reported by Gonzalez et al as other ecological services [85]. The *Oecophylla* ants validated the dual pollinator-nectar protection hypothesis by permanent daylight foraging behavior. The Asian weaver ants in South-East Asia and tropical Australia represent a strategic potential influence on the ecological and evolutionary paths of plant-pollinator interactions [86].

A comprehensive study needs to be done on the findings of supervision function among *O. smaragdina* workers by including an investigation of canopies colonies' overall activity.

The study of ant swarm intelligence did open a wide avenue to solve a load of problems for industrial applications for example the foraging behavior of the *Pachycondyla apicalis* ants inspired the resolution of diverse algorithms [87].

5. Conclusion

The *Oecophylla* ant's daily foraging activity inside of sizable oil palm plantations in connection to weather parameters is being studied for the first time over a long period. The results of this study, which demonstrate that major workers are solely diurnal-predator active foragers constantly throughout the day under clear weather conditions, corroborate those of earlier reports. Regarding our results, we can conclude that:

1. The time that coincided with the warmest day periods and the abundance of colonies had a bimodal pattern and intensity for daily foraging activity.
2. Only the daily observation of both trunk and ground foraging behaviors could result in a more accurate study of the weaver ants because the tropical climate was stable and there were no extreme weather parameter fluctuations. However, canopies foraging activity is an important component
3. The organization of leaders among major workers exhibiting the supervision function of smaller workers during trail activity on the main trunk is a first case report for social insects in general.
4. Major workers' daily foraging activity monitoring exposed their strictly diurnal behavior status. The absence of light directly impairs and makes the ants inactive foragers.
5. Temperature, atmospheric pressure, the amount of precipitation, and relative humidity are among the main weather factors influencing weaver ant major workers' daily activities.

6. The partial forager daily short periodic activity halt (intensity reduction) corresponds to a first ever such finding. As an obligate arboreal species, weaver ants showed a strong propensity for ground-dwelling behaviors, with consecutive territorial defense layers extending 5 m from the trunk. It had two different geographic configurations. Major workers' trunk trails diverged into multiple new lines at intervals of about 3 m, indicating a greater foraging density. The tracks diverged to form a web-shaped occupation that extended an average distance of 5 m.

The combination of an extensive foraging activity array covering occupied areas with the systematic predatory behaviors towards many insect pests does explain the successful protection services provided by *O. smaragdina* in agro systems. Our recommendations for plantation workers to work during the times of day with the least amount of ant activity work from sunrise until before 1000 h for Peninsular Malaysia and 0930 h for Borneo Sabah/Sarawak. Finally, in the case of weaver ants being adopted for biological control or by Integrated Pest Management strategy, this would minimize bite exposure.

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Data availability

All data are submitted and available to the following deposited links:

<https://data.mendeley.com/datasets/pmphy8gxp7> <https://data.mendeley.com/datasets/4pcn2r3s7k> <https://doi.org/10.13140/RG.2.2.22876.05763> <https://doi.org/10.13140/RG.2.2.36297.83044>.

- DOI: 10.13140/RG.2.2.33505.28000/1.

CRediT authorship contribution statement

Moïse Pierre Exéllis: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rosli Ramli:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis. **Samshul Amry Abdul Latif:** Writing – review & editing, Software, Methodology, Formal analysis. **Azarae Hj Idris:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis. **Gemma Maria Clemente-Orta:** Writing – review & editing, Methodology. **Claire Kermorvant:** Writing – review & editing, Software, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.heliyon.2024.e26105>.

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